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Prospective generalist invertebrate  
predators for conservation biological  
control of the vineyard pests  
*Epiphyas postvittana* and  
*Pseudococcus calceolariae*.

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A thesis submitted in partial fulfilment of the  
requirements for the  
Degree of Doctor of Philosophy  
at Lincoln University  
by  
Benjamin M. Hancock

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Lincoln University

2015

To Ariella

“There is a theory which states that if ever anyone discovers exactly what the Universe is for and why it is here, it will instantly disappear and be replaced by something even more bizarre and inexplicable. There is another theory which states that this has already happened.”

– Douglas Adams, *Hitchhiker's Guide to the Galaxy*, 1980

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**Abstract**

A series of field surveys and experiments were performed to identify generalist invertebrate predators which could complement the parasitoid *Dolichogendia tasmanica* in management of the vineyard pest *Epiphyas postvittana* and an additional pest *Pseudococcus calceolariae*.

Conventional agricultural methods have been able to improve food production but some practices have been at the cost of ecosystem services, and beneficial services derived from the ecosystem. A dependence on agro-chemicals to maintain production can develop in order to substitute for services that have been lost, threatening the long-term sustainability of production. Biological control is one

of these ecosystem services which can be employed in place of chemical pesticide inputs and, with prudent investigation, can maintain productivity and improve sustainability.

Conservation biological control (CBC) is a form of biological control that utilises natural enemies from within the ecosystem, circumventing some of the issues traditionally associated introducing a new species with classical and augmentative biological control. Another advantage of CBC is that generalist natural enemies are potentially more acceptable to include in pest management. Traditionally, generalists have been deemed unsuitable in biological control but there could be potential as an early-season management tool to complement existing *E. postvittana* biological control in vineyards with *D. tasmanica*. Additionally, there may be an advantage of generalist predators attacking a second vineyard pest, *Ps. calceolariae*.

To begin to identify those generalist natural enemies that may be incorporated in vineyard pest management, predator surveys of the ground and canopy of twelve organic and conventional vineyards were carried out from 2010 to 2012 in Marlborough, New Zealand. Sentinel bait cards with *E. postvittana* larvae or eggs were placed throughout the vineyards and the predator species attacking the pest and comparative removal rates were observed. To determine which vineyard predators of *E. postvittana* could attack both pest species, maximum consumption rate experiments with *E. postvittana* larvae and eggs, along with adult females and nymphs of *Ps. calceolariae*, were carried out in laboratory arenas. Subsequently, experiments were carried out in vine canopy cages to investigate interactions between the predator species and the prey preferences of predator species. Individuals of each predator species that attacked both pest species in

laboratory experiments were presented with a pairwise choice of *Ps. calceolariae* nymphs and *E. postvittana* larvae or eggs to test for any prey preference by the predator species. In experiments examining inter-specific predator interactions, each combination of predator species was presented with the different prey types where a variation from the null hypothesis indicated non-linear relationships (antagonism or synergism).

Three predator species were observed attacking *E. postvittana* eggs and larvae on bait cards in the vineyard canopy; *Anystis baccarum*, *Forficula auricularia*, and *Phalangium opilio*. Functional predator diversity was higher in organic vineyards, but no difference in prey removal rates of *E. postvittana* eggs or larvae between conventional and organic vineyards was observed. In laboratory trials, *F. auricularia* killed more of each prey type than the two other predator species, and was the only predator species to predate on all prey types of both pest species. *P. opilio* consumed both *E. postvittana* prey types plus *Ps. calceolariae* nymphs. Although *A. baccarum* consumed only *E. postvittana* eggs in laboratory trials, despite attacking larvae on bait cards in the vineyards, their consumption rate was not significantly different from that by *P. opilio*. Only *F. auricularia* and *P. opilio* were used in prey preference experiments, as *A. baccarum* consumed only one prey type in the laboratory. *F. auricularia* showed no preference between *Ps. calceolariae* nymphs, *E. postvittana* larvae or eggs; however *P. opilio* did display a preference for *E. postvittana* eggs over larvae but no preference between pest species was observed. When all three predators were combined as an assemblage, a consistent additive effect on predation across *Ps. calceolariae* nymphs, *E. postvittana* larvae and eggs was observed. *F. auricularia* interacted antagonistically when combined with either of the alternative predator species and presented with *E. postvittana* eggs, and again with the predator *P. opilio* and *Ps. calceolariae* nymphs as prey.

*E. postvittana* larvae predation was higher than hypothesised in both pairwise predator combinations that included *A. baccharum*.

Not one of the three predator species identified as potential CBC agents of *E. postvittana* in vineyards can be ruled out, but a range of potential strengths and limitations was identified. *F. auricularia* predated on all pest prey that was presented, and consumed more of each prey type than the other predator species. However, the negative interactions with the alternative predators could diminish improvements to pest control gained by promoting this species for biological control. *A. baccharum* had the most limited range of prey but was the most frequently observed attacking *E. postvittana* in vineyards and could be effective mitigating non-additive interactions between other predators', including prey which this predator was not observed predated on. The preference of *P. opilio* for *E. postvittana* eggs over larvae indicates potential complementarity with *D. tasmanica*, a larval parasitoid, as overlap in prey use could be reduced. While *P. opilio* was, comparatively, not a voracious predator of the pest species, it did predate on both species.

The observations made here can be used to progress investigations of these predator species as CBC agents. How these candidates perform and interact with other species in unrestricted vineyard systems and the nature of interactions with the *E. postvittana* parasitoid *D. tasmanica* are two key areas to pursue. The final outcome will be developing practices that provide service providing units (SPU) for managing *E. postvittana* and *Ps. calceolariae* that improves crop yield and quality. There was evidence that *A. baccharum*, *F. auricularia*, and *P. opilio* can potentially complement *D. tasmanica* to this effect.

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# Chapter 1

## Introduction

### 1.1 Sustainable production

The challenge of increasing food production to meet demand of a growing global population is exacerbated by challenges to maintaining productivity and shifts in desired food stuffs. The global population has doubled in the last 50 years and is expected to continue growing to around 9.6 billion in the next 50 years and 10.9 billion at the end of this century (Gerland et al., 2014). More food will need to be produced from the same land area without further degradation of the environment and continued heightening of the risks to production often associated with conventional intensive and industrial food production methods (Godfray et al., 2010; Pretty, 2013; Pretty and Bharucha, 2014; Tilman et al., 2011). Feeding the world's increasing population is further complicated by increased wealth and growing global middle class in populous nations, such as China, raising demand for diet of increased energy, higher in protein, and improved quality and security (Garnett et al., 2013; Kastner et al., 2012; Kuyper and Struik, 2014). However, distribution and waste of food also remain important factors in global hunger (Pretty and Bharucha, 2014; Tscharnkte et al., 2012).

As global agricultural production has increased, unsustainable land use practices have contributed to pressure on maintaining production. Intensive agriculture has led to the homogenisation of large areas the earth's surface to the detriment of natural habitats and biodiversity as the demand for production has increased (Gabriel et al., 2013; Tilman et al., 2002; Matson et al., 1997). Some conventional practices have compromised long-term production through soil degradation and erosion, over-exploitation and improper water use, along with non-production driven changes like urbanisation (Brussaard, 2013; Godfray et al., 2010; Lang, 2010).

Beneficial goods and services derived from ecosystem function and biodiversity within an ecosystem are termed ecosystem services (Costanza et al., 1997; Hooper et al., 2005; Luck et al., 2003). Low biodiversity can reduce ecosystem services, leading to practices such as pesticides applications, which in turn reduces future biodiversity (Altieri, 1999; Naeem et al., 1994; Tilman et al., 2002). This approach has been termed substitution agriculture because damaged or lost ecosystem services are substituted by fossil fuel derived fertilisers and pesticides (Rosset and Altieri, 1997).

The widespread use of agro-chemicals (fertilisers, pesticides) that provide immediate gains has become part of modern conventional intensive agriculture but have also been a major contributor to those issues that threaten global production (Alexandratos, 1999; Tilman et al., 2002). There is many examples of where advantageous agro-chemicals have had unintended human and environmental consequences to the detriment of biodiversity and ecosystem services; for example bio-accumulation of dichlorodiphenyltrichloroethane (DDT) (Spencer et al., 1996;



Turusov et al., 2002), neonicotinoids impact on pollinators and birds (Girolami et al., 2009; Hallmann et al., 2014; van der Sluijs et al., 2013), organophosphates (Eskenazi et al., 2004; Nasrabadi et al., 2011) and other endocrine disruptors (Colucci et al., 2001). This is not to say that the use of agro-chemicals is misguided, only their imprudent use, and they will continue to be part of a managers “toolbox” needed to sustain production. Land that has been degraded can sometimes maintain production with increased inputs via these substitutive methods (Tilman et al., 2002). Advancements in conventional agriculture over the previous 65 years have certainly contributed to alleviating global hunger (Kuyper and Struik, 2014; Matson et al., 1997; Tilman et al., 2002).

Yet, there is potential within the diversity of the local environment that can be incorporated into agricultural practices to improve management and sustainability of production. Due to the complexity of these services and that they are intrinsic features of an environment, estimating the value of these benefits is difficult leading to under appreciation and lack of consideration (Losey and Vaughan, 2006). Utilising ecosystem services can improve the sustainability of agro-ecosystems, and protect future availability of resources while maintaining yields and providing economically viable alternatives that reduce chemical inputs (Godfray et al., 2010; Matson et al., 1997; Porter et al., 2009; Sandhu et al., 2015).

The different pressures surrounding sustainable agriculture production can be divided into top-down and bottom-up influences. Factors that contribute to top-down influences are usually from government or industry legislation, market demand, and cultural limitations. These can include governmental policy, preserving food security, chemical withholding periods and residual restrictions, industry directives, market access, price premiums for sustainable production, enhanced

revenues from environmental amenities and tourism (Geiger et al., 2010; Manktelow et al., 2005; Mollá-Bauzá et al., 2005; Tompkins and Mason, 2008; Wandel and Bugge, 1997). Bottom-up influences are those involved with production and working within the limitations of the environment. These production pressures are driven by; maintaining or improving yields, minimising inputs and costs, preventing system degradation, pesticide/herbicide resistance, sustainable and efficient use of available resources, and mitigating risks to production, environment and staff (Altieri, 1999; Hobbs et al., 2008; Sandhu et al., 2015; Tilman et al., 2002). For adoption of sustainable agricultural practices there needs to be a combination of social, cultural and market pressures, relevant scientific research directed at minimising or replacing chemical applications, and development of sustainable production management protocols that are proven effective and economic (Cullen et al., 2008; Sandhu et al., 2008).

## **1.2 Biological control**

Biological control is an ecosystem service that can be provided by the existing environment or introduced organisms to manage species that are detrimental to agricultural production or culturally important environments. Application of this ecosystem service employs biotic elements in the environment to reduce or limit weeds, pests and diseases in cultural and production systems (Eilenberg et al., 2001). Biological control is not the sole solution for pest management but one tool in an arsenal of techniques for integrated pest management (Birkhofer et al., 2008b; Gurr et al., 2004; Lewis et al., 1997). Costanza et al. (1997) estimated biological control to be an ecosystem service worth over US\$ 400 billion per year world wide, land use change has contributed to continual decline of ecosystem services since this estimate (Costanza et al., 2014) . Within the United States

of America, four ecosystem services provided by insects (pest control, pollination, recreation and dung burial) have been valued at US\$ 57 billion per year (Losey and Vaughan, 2006).

The use of chemical pesticides as part of intensive agricultural management have been shown they can be to the detriment of the surrounding environment. Not only negatively impacting on the sustainability of agricultural production and ecosystem services, but culturally valued features of the environment (Altieri, 1999; Krebs et al., 1995; Kuyper and Struik, 2014). The negative effects of reliance on substitution agriculture can include; the pest and predator/parasitoid relationships becoming unstable which heightens susceptibility to pest irruptions (Yardim and Edwards, 1998), degradation of ground and surface water (Tilman et al., 2002), diminished pollination by insects (Mullin et al., 2010), reduced alternative host/prey and beneficial invertebrate populations (Harwood et al., 2009), and increased the likelihood of accidental poisoning (Aktar et al., 2009).

Biological control can be classified into three different groups. Conservation biological control (CBC) is a method of biological control that engineers the environment to benefit survival, longevity, fecundity and behaviour of naturally occurring predators, parasitoids and pathogens of pests (Eilenberg et al., 2001; Landis et al., 2000). The alternative forms of biological control are classical (introduction and establishment of a new species), and augmentative (inoculative or inundative, where early or numerically large releases of an agent temporarily limits pests) (Eilenberg et al., 2001; Gurr and Wratten, 1999).

Classical biological control is often seen as the standard form of biological control. This method is often used to manage introduced species that have become

naturalised and a nuisance in a new environment, with a natural enemy from the pest species native range (Bale et al., 2008; Eilenberg et al., 2001). When successful, classical biological control can provide a long-term service that inhibits the pest and has little or no on-going costs and management, often in established perennial systems (Bale et al., 2008; Louda et al., 2003).

Classical biological control requires a comparatively greater initial economic cost and time to research. This method can be very cost effective when successful but failure is potentially an expensive exercise (Bale et al., 2008; Gurr and Wratten, 1999). The likelihood of success has historically been low globally at 10.8%, a conservative value as failures are less likely to be reported (Greathead and Greathead, 1992; Louda et al., 2003). Classical biological control within New Zealand has had even lower achievement, ranking fourth in the total number of recorded biological control introductions, 29.3% have established and only 8.7% were successful in controlling the target pest (Greathead and Greathead, 1992). The desirable traits of classical biological control agents (ease of establishment, high dispersal, and population persistence) can become negative if they have unintended impacts such as affecting non-target species or moving into other ecosystems and require removal or on-going management (Louda et al., 2003).

Augmentative biological control is a variation with different advantages to be weighed against the costs and risks. Where classical biological control introduces a novel organism that establishes a self-sustaining population that controls the pest, augmentative control requires ongoing inoculative or inundative releases (Bale et al., 2008; Collier and van Steenwyk, 2004). Inoculative introductions involve releases to establish a population of the biological control organism when seasonally required that perpetuates itself to manage the pest but does not persist

in the environment as a classical biological control introduction (Eilenberg et al., 2001). An inundative release is of a numerically large number of organisms that interrupt the pest population at release to limit pest damage, but the biological control agent has very limited or no ability to sustain a population (Eilenberg et al., 2001).

Augmentative biological control is not a cheap method of control. This form needs significant up-front and continual expenditure for infrastructure, propagation of the control agent, and monitoring of the pest species to determine necessary intervention, along with similar pre-release research and risk analysis to classical biological control (Collier and van Steenwyk, 2004, 2006). The benefit of augmentative releases is the use of species that are not able to persist in the target environment or maintain a population that is effective at controlling the pest species. The liabilities associated with classical biological control agents affecting non-target species or dispersing into undesired ecosystems are mitigated, and the risk of on-going management or species eradication are removed (Eilenberg et al., 2001).

### **1.3 Conservation biological control**

There has been a general shift away from high investment and high risk forms of biological control towards looking at utilising natural enemies that are already present in the environment (Jonsson et al., 2008; Symondson et al., 2002). CBC provides a lower risk and potentially cheaper method of pest control. This method of pest management can help to address problems created by agriculture intensification and future demand, while addressing concerns of the alternative biological methods (Bale et al., 2008; Jonsson et al., 2008). Natural enemies can be pro-

moted by increasing activity and fecundity or minimising mortality through providing refuge, reducing secondary enemies, supplying alternative or higher quality nutrition (Landis et al., 2000). The key element of CBC in utilising organisms within the environment negates many of the risks involved in the two alternative types of biological control, minimising the initial expense and investment required.

Development of CBC focuses on identifying the suitable agents within the environment that are detrimental to target species by promoting the biological control agent without benefiting pest species and impairing production or cultural values (Cullen et al., 2008; Jonsson et al., 2008; Landis et al., 2000). Unlike classical biological control, CBC requires on going management within the target ecosystem and can be the more labour intensive option (Cullen et al., 2008). However, this ongoing management does not require the same level of infrastructure and detail of pest monitoring as the augmentative method since the biological control agent and management are carried out in the ecosystem (Jonsson et al., 2008).

Four characteristics have historically been used to determine the suitability of a biological control for a classical biological application; 1) high reproductive rate, 2) good dispersal, 3) high degree of prey/host specialisation, and 4) ability to naturalise to the desired environment (Chang and Kareiva, 1999; Symondson et al., 2002). High fecundity and good dispersal ability are desired characteristics in that the biological control agent is able to respond to increases of the pest species population. Prey or host specificity is important in considering the risk of introducing a novel species into a new environment to preclude any unintended impacts and is desired so the biological control agents effort is diverted away from the pest species. This characteristic is partially addressed by using CBC, as the potential control organism is already present, and the likelihood of any new associations with flora and fauna is limited. For the same reason, capability to adapt to

the required environment is negated, though a key point in development of CBC shifts to identifying constraints of the environment to benefit the natural enemy.

Acceptance by producers is important for adoption of biological control in agricultural systems, more so in CBC than other biological control methods. CBC demands more of farmers and managers in terms of time spent, on-going management and restricting other practices that may affect the biological control agents (Cullen et al., 2008). Including producers in the development of techniques coupled with dissemination of economic and efficacy analyses are needed to improve up-take of new practices (Cullen et al., 2008).

In a broader sense, CBC has greater potential for innovation and adoption in less developed regions. Access to technology, knowledge and finances are major contributors to the gap between actual and potential yield in developing nations, which is exaggerated in socially unstable regions (Godfray et al., 2010). Creating management techniques that require less investment of resources would be more readily incorporated in production systems in these areas. Successful CBC could control pests without the issues of logistics, infrastructure, risks and costs associated with augmentative or classical biological control (Cullen et al., 2008; Sunderland and Samu, 2000).

## **1.4 Generalist predators as CBC agents**

Traditionally, biological control desired traits associated with specialists natural enemies but there is also potential in generalist species, particularly when incorporated with CBC. A high degree of host or prey specificity or oligaphagy has often historically been deemed necessary to ensure that unintended impacts on beneficial and desired species are negligible, and foraging or parasitising effort

is concentrated on the target pest (Chang and Kareiva, 1999; Symondson et al., 2002). Three perceived limitations of generalists as biological agents are; 1) slower numerical response to pest arrival and irruptions because of generally slower reproductive rates, 2) pest removal effort can be reduced by the presence of alternative prey, and 3) predation rate per individual is comparatively low to generally more specialised parasitoids due to handling time and satiation (Sabelis, 1992). These shortcomings are mostly relevant from the perspective of classical or augmentative biological control, and the significance of these obstacles decrease in a CBC setting and can be advantageous. Symondson et al. (2002) produced a comprehensive review that covered the concerns and benefits of employing generalists in biological control.

An advantage of generalist natural enemies is their ability utilise a wider range of prey and populations can be more persistent over time. While they may not be as responsive numerically to prey irruptions, generalists may provide a stable form of control as a "lying-in-wait" strategy and early season pest control that suppresses pest populations (Boreau de Roince et al., 2013; Settle et al., 1996; Symondson et al., 2002). The availability of alternative prey and reduced reliance on the pest species gives generalists the ability maintain their population as the pest population is reduced or even locally extinct and in stressed times such as winter (Chailleux et al., 2014; Chang and Kareiva, 1999; Settle et al., 1996). Management strategies that promote refuge and overwintering sites often increase biodiversity, benefiting persistence of generalist species with alternative habitat and food sources (Danne et al., 2010; Symondson et al., 2002; Tompkins and Mason, 2008) Due to the generalist species population not tracking the pest's, their ability to suppress and control the pest outright is limited but generalists have been shown to impede pest population increase (Boreau de Roince et al., 2013;



Chailleux et al., 2014; Chang and Kareiva, 1999; Snyder and Ives, 2003).

Pea aphids (*Acyrtosiphon pisum* (Homoptera: Aphididae)) were able to be suppressed with a specialist parasitoid, *Aphidius ervi* (Hymenoptera: Braconidae), but only after aphids reaching high densities (Snyder and Ives, 2003). Whereas, generalist predators impacted aphids at lower densities and slowed population increase (Snyder and Ives, 2003). This combination of a persistent generalist that dampens pest irruptions to allow time for the specialist’s population to respond and suppress the pest species with reduced pest population peaks. Early season control by natural enemies can also reduce the spread of plant disease, an effect which can persist throughout the season (Landis and van der Werf, 1997). Improving the quality overwintering habitat for natural enemies is a pathway that could improve the efficacy of generalists in this potential mode of pest control (Gardiner et al., 2009).

## 1.5 Generalist natural enemies in assemblages

Integrating generalist natural enemies into biological control assemblages of species can improve the rate of pest removal. A diversity of habitat use and mode of attack by natural enemies can increase pest control more than what would be expected by simply adding species together. Schmitz (2007) produced four models of outcomes using assemblages based on a synthesis of experiments that looked at interactions between natural enemies when utilising the same prey or host (Figure 1.1).

Positive interactions between natural enemies of the pest species can be synergistic/risk enhancing (e.g. attacking behaviour of one species making the pest more prone to another species) or additive/complementary (e.g. diversity of

hunting modes or habitats between natural reduces potential refuges for the pest species) (Schmitz, 2007; Sih et al., 1998; Snyder and Ives, 2001). The two preferred outcomes could apply to using a combination of a generalist (predator) and a specialist (parasitoid) (Figure 1.1, a), or an assemblage of generalists (Figure 1.1, b).

Paull et al. (2012) presented an example of short term risk-enhancement when combining a generalist predator *Anystis baccarum* (Acari: Anystidae) with a parasitoid, *Dolichogenidea tasmanica* (Cameron) (Hymenoptera: Braconidae), as anti-parasitism behaviour by *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) was to leave refuges and became more prone to predation. However, modelling suggested this could be detrimental to the parasitoid on a longer time scale as recruitment is reduced by the predator (Paull et al., 2012). Hogg et al. (2013) observed negative impacts by a spider, *Cheiracanthium mildei* (Araneae: Miturgidae) on an *E. postvittana* parasitoid population, *Meteorus ictericus* (Hymenoptera: Braconidae), but an overall additive effect of *E. postvittana* mortality due to higher parasitism ability of the parasitoid and no predator preference for parasitised prey.

An additional limitation of generalist predators that may occur in biological control are the behavioural challenges of intra-guild predation, inter-specific interference and cannibalism (Rosenheim, 2001; Symondson et al., 2002). Schmitz (2007) suggests that increased overlap in hunting mode and habitat use heighten interference and intra-guild predation (Figure 1.1, c, d). These interactions would have to be examined case by case, for example, even with the occurrence of intra-guild predation the overall result of an assemblage predators and parasitoids can still benefit pest removal (Chailleux et al., 2013; Hogg et al., 2013; Snyder and Ives, 2003). Occurrence and importance of these behavioural interactions would

need to be investigated when determining suitability of a species for biological control.

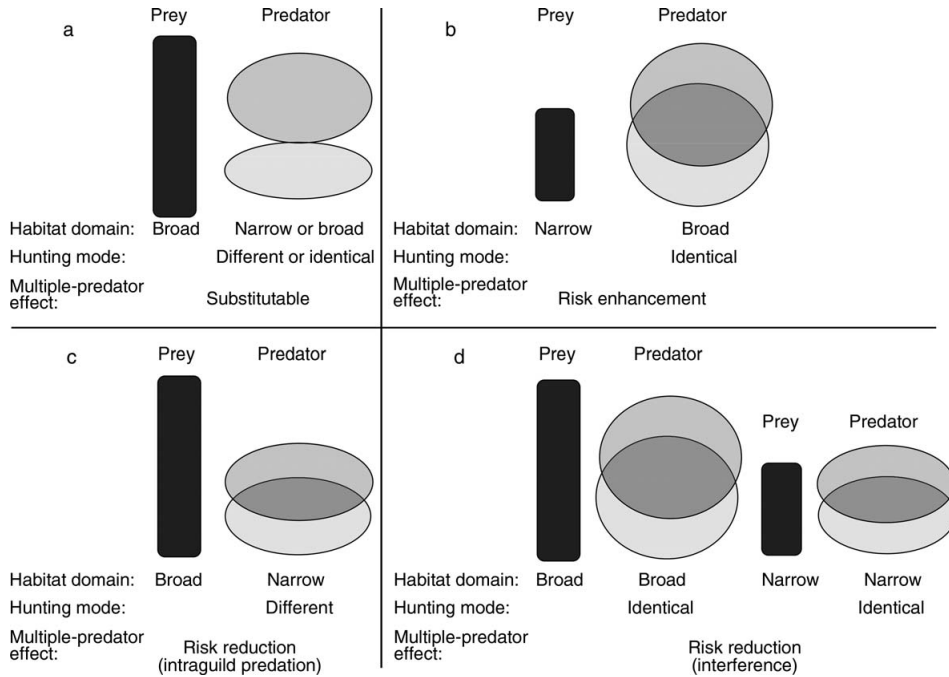


Figure 1.1: Predictions of four contingent multiple-predator effects on a common prey species derived from an empirical synthesis of multiple-predator experiments. Dark rectangles represent the prey habitat domain. Ellipses represent predator habitat domain. (a) Predators are expected to have substitutable effects whenever prey have broad habitat domains and predators have complementary (narrow or broad) habitat domains. (b) Predators are expected to have risk-enhancing effects whenever prey have a narrow domain and predators have broad, overlapping habitat domains and the same hunting modes. (c) Predators are expected to have risk-reducing effects due to intraguild predation whenever prey have a broad domain and predators have narrow, overlapping habitat domains and different hunting modes. (d) Predators are expected to have risk-reducing effects due to interference interactions when they have identical hunting modes and overlapping habitat domains with themselves and their prey (Schmitz, 2007).

The concern of slow population response to increases in pests and satiation can be counteracted by behaviours of generalist predators. Generalists can contribute more to pest removal than what they consume, as there have been observations of

wastefully killing without consuming prey (Riechert and Maupin, 1998; Symondson et al., 2002; Thies et al., 2011). Also, if the prey is unpalatable then generalists may kill the prey then disregard them or partially consume prey at high densities, only consuming the readily available prey contents (Fantinou et al., 2008; Sunderland, 1999). Disturbance by predators can compel prey to drop or move out of refuge leaving them prone to other predators or desiccation (Symondson et al., 2002; Takada et al., 2013).

A combination of wasteful killing at higher prey density, early season predation with improved overwintering ability, and the capacity to use alternative prey species make generalist predators an attractive potential biological control agent. Generalist species can offer alternative advantages over specialist predators and parasitoids. Chang and Kareiva (1999) and Symondson et al. (2002) present examples where generalist natural enemies have played a bigger role in controlling pests despite the presence of specialists, highlighting the opportunities and necessary consideration generalists deserve. Generalists demand attention as biological control agents because of their potential to maintain their population throughout the year, decreased reliance on the target pest for population persistence, improve ecosystem stability, and early-season impact on pest populations (Chang and Kareiva, 1999; Dunne et al., 2002; Östman et al., 2001; Symondson et al., 2002). This not to say the generalist are superior for biological control, but an alternative or complementary tool to specialist biological control agents (Chailleux et al., 2013).

## 1.6 The New Zealand wine industry

As the global population and wealth continues to grow in some regions over this century, pressure for more affluent food products such as processed food, meat, dairy and wine will also grow (Bisson et al., 2002; Godfray et al., 2010; Kastner et al., 2012). Globally, New Zealand wine exports have a small yet valuable niche in this discerning market.

New Zealand is not a significant producer on the global market but does produce relatively high value wine. Of the 9.8 billion litres produced internationally in 2013, New Zealand only contributed 248.4 million litres (2.54% of global production) of which 68.3% is exported, worth NZD\$1.21 billion (New Zealand Winegrowers, 2014; OIV, 2014). In the United Kingdom, New Zealand's third biggest wine export market of 2013 by revenue (NZD\$278.415 mil, NZD\$5.85/litre), was second only to France in price per volume (New Zealand Winegrowers, 2014; OIV, 2014). The price per volume was even higher in New Zealand's two largest export markets by revenue, Australia (NZD\$373.048 mil, NZD\$7.50/litre) and USA (NZD\$283.651 mil, NZD\$6.54/litre), and these three markets accounted for 82.95% volume exported (New Zealand Winegrowers, 2014).

Within New Zealand, the most widely grown variety in 2012 was Sauvignon Blanc (20,270 ha, 57.4%) which accounts for 85.5% of New Zealand's wine export volume (New Zealand Winegrowers, 2014). Sauvignon Blanc production is followed by Pinot Noir (5,388 ha, 15.2%) and Chardonnay (3,229 ha, 9.1%). The Marlborough province in the north-east of the South Island is the largest producer of wine (22,956 ha, 2012), with the Hawke's Bay in the eastern North Island a distant second (5,030 ha) (New Zealand Winegrowers, 2014).

The top-down pressures of sustainable production are not exempt in the wine industry, and in this discriminating market there are competitive incentives. Sustainable and environmentally sound production of wine has become an important consideration of wine consumers and an indication of quality (Bisson et al., 2002; Warner, 2007). Implementing integrated pest management and highlighting sustainability in wine production provides a competitive marketing edge, particularly at the high-price end of the range (Bisson et al., 2002; Bray et al., 2002; Warner, 2007). Consumers surveyed in Spain were willing to pay 16% more for organic wine, or 14% of the population who are more likely to identify as having a healthy lifestyles, environmental concern and higher education would pay 25% more (Mollá-Bauzá et al., 2005). These observations could well be expected to occur in other markets that are more important to New Zealand wine exports (Cullen et al., 2008; Forbes et al., 2011). Improving biodiversity in agricultural settings is not solely limited to economic benefits but also non-monetary incentives. These non-market justifications can include ethical and aesthetic reasons (Hooper et al., 2005; Naeem et al., 2015), and, while seemingly altruistic in a commercial system, can still provide financial advantages like eco-tourism to attract customers to the winery and raising brand profile (Fountain and Tompkins, 2011; ?). CBC is economically attractive for the production of wine because of the maintained grape production quality and access to premium markets with less upfront investment for pest control as other biological control types (Cullen et al., 2008; Forbes et al., 2011).

While adherence to industry standards such as Sustainable Winegrowing New Zealand<sup>®</sup> (SWNZ), which independently audits industry agreed guidelines of not only chemical and water use in wineries and vineyards but also staff and waste management, or organic BioGro<sup>™</sup> New Zealand Ltd certification are constructs of

top-down pressure, the ubiquitous industry acceptance creates a minimum standard for wine grape production in New Zealand. In 2014, 94% of New Zealand’s wine producing area was certified as sustainable or organic (New Zealand Winegrowers, 2014). Production in accordance with audited programs is often required for entry into industry and export showcases. Industry standards such as SWNZ provides mechanisms to educate and market “green” products to consumers, enhancing the country’s premium position on the global market (Forbes et al., 2011; Fountain and Tompkins, 2011; Kim and Bonn, 2015).

Whichever agro-ecosystem is investigated with a view to enhance ecosystem services, the principles, protocols and service providing units are potentially applicable to other agro-ecosystems (Luck et al., 2003). Viticulture will not feed the world but can act as a model system for other mono-cultures. Conventional vineyard management produces mono-cultures that are comparatively low in biodiversity compared to other ecosystems in similar latitudes, limiting the potential ecosystem services available (Nicholls et al., 2008). By establishing CBC methods in this simplified system, the techniques and knowledge can be transferred into other production systems.

## **1.7 New Zealand vineyard pests of concern**

Naturally occurring biotic regulators of have benefited from changes in chemical use within New Zealand. A shift from broad-spectrum pesticides to judicious and less frequent use of selective insecticides due to industry implementation of sustainability programmes can lead to increased parasitism of pests (Manktelow et al., 2005; Varela et al., 2008). The current use of targeted pesticides in New Zealand is primarily to control leafroller and mealybug pests (Manktelow et al.,

2005). Addressing these pest species with biological control has a greater potential to reduce pesticide use in vineyards.

### 1.7.1 *Epiphyas postvittana*

The light brown apple moth (LBAM) (*E. postvittana*) is a costly widespread pest and predominant leafroller in New Zealand vineyards (Lo and Murrell, 2000; Tooman et al., 2011). Suckling and Brockerhoff (2010) produced a comprehensive synthesis of the biology, ecology, pest impact and management of *E. postvittana*. *E. postvittana* is a polyphagous pest in agricultural and horticultural systems, predominantly of fruit crops but is also present in silviculture, ornamental and vegetable crops (Suckling and Brockerhoff, 2010). In vineyards, *E. postvittana* not only causes damage by consuming leaves and young shoots but directly impact on yield by feeding on flowers, stalks and berries (Lo and Murrell, 2000). Grapes damaged by *E. postvittana* larvae become prone to infections that degrade the quality of the wine, such as the fungus *Botrytis cinerea* (Helotiales: Sclerotiniaceae), and larvae can increase transmission of fungus pores (Bailey et al., 1997; Barata et al., 2012).

*E. postvittana* has been invasive globally and is a well studied pest species. Originally from south-eastern Australia, *E. postvittana* has been found on a range of native and introduced plant species across multiple states (Danthanarayana, 1975). Early records of *E. postvittana* in New Zealand show a relatively recent establishment after European colonisation in the 19th Century (Suckling and Brockerhoff, 2010). Currently, this pest species has established elsewhere around the Pacific (Japan, Hawai'i and potentially New Caledonia), North America (California), the British Isles (England, Wales and Ireland), Scandinavia (Sweden) and Europe



(Netherlands) (Danthanarayana, 1983; Suckling and Brockerhoff, 2010; Tooman et al., 2011). The wide range of host species, economic risk and invasability can create trade limitations for exports (Varela et al., 2008), though this concern is not an issue for wine trade as *E. postvittana* does not persist through the production process.

Between two and three generations of *E. postvittana* per year have been observed across the wine producing latitudes of New Zealand (Suckling and Brockerhoff, 2010). In Australia, the generations have been detected at nearly five per year (Mo et al., 2006). Larvae will form a silken refuge (hibenaculum) soon after emergence from eggs in recesses and leaf rolls of vines where they will feed until pupation (Paull et al., 2012). These refuges can inhibit predation of larvae (Paull et al., 2012).

### 1.7.2 Mealybugs (Hemiptera: Pseudococcidae)

The citrophilus (*Pseudococcus calceolariae* (Maskell) (Hemiptera: Pseudococcidae)) and long-tailed *Ps. longispinus* (Targioni-Tozzetti) mealybugs can account for nearly all of mealybugs detected in vineyards, and are present throughout New Zealand’s wine producing regions (Charles et al., 2010). Like *E. postvittana*, *Ps. calceolariae* and *Ps. longispinus* are polyphagous pests of not only vineyards, but a variety of other horticultural crops (Charles, 1993; Wakgari and Giliomee, 2003; Zaviezo et al., 2010). Work produced by Charles et al. (2010) and Charles (1982, 1993) has covered mealybug damage, distribution, economic impact and management in New Zealand. Daane et al. (2012) composed a synthesis of a wider range mealy bug species in vineyards globally. Very rare detections of the exotic *Pseudococcus viburni* (Signoret) and native *Paracoccus abnormalis* (Cox) have occurred

in New Zealand vineyards (Charles et al., 2010)

Mealybugs are ubiquitous and persistent pests for grape production internationally. Both *Ps. calceolariae* and *Ps. longispinus* are indigenous to Australia and arrived in New Zealand incidentally (Charles et al., 2010). Now these species are widespread vineyard pest species, present in; Europe, North America, South America, and South Africa (Daane et al., 2012). Many other mealybug species (*Pseudococcinae spp.*) are classified as pests in other wine producing countries and are increasing as an issue in vineyards globally (Daane et al., 2012; Hardy et al., 2008). However, like *Ps. calceolariae* and *Ps. longispinus* they are not limited to being a concern in vineyards but other horticultural crops too (Hardy et al., 2008).

Mealybugs overwinter in the soil on the roots of vines or under the bark, moving out on to the foliage when vine growth begins into less exposed and recessed positions, such as abaxial side of leaves, inside fruit bunches and cracks in the trunk (Charles, 1982; Charles et al., 2010; Lo and Walker, 2011). There is generally between two or three generations in New Zealand grape growing conditions (Charles, 1981; Charles et al., 2006). Unless at high density, where mealybugs may affect the quality of the wine (Charles, 1982), the main concern is spreading Grapevine Leafroll-associated Virus 3 (GLRaV-3) (Daane et al., 2011; Petersen and Charles, 1997).

Grapevine Leafroll disease (GLR) is a pervasive disease affecting grapevines. The disease has serious economic consequences as it can reduce wine quality by slowing bud break, flowering, and fruit ripening; lowering sugar content and increasing acidity in fruit; and decreasing vine yield (Charles et al., 2006; Credi and Babini, 1997; Mannini et al., 1997). The disease can be introduced into vineyards

via grafting, though not by machinery or vine management activities, and young vines can act as a source of the disease as they do not show symptoms (Charles et al., 2009).

GLR is a complex of at least seven viruses, of which GLRaV-1 and GLRaV-3 are more associated with GLR (Daane et al., 2012; Choueiri et al., 1996). GLRaV-3 has been shown to be the most common of the two viruses in New Zealand, as GLRaV-3 it was present in 96.5% of GLR infected vines and 3.5% vines with GLRaV-1 (Petersen and Jordan, 1992). Of the two viruses only GLRaV-3 can be vectored by *Ps. calceolariae* and *Ps. longispinus* which are the primary causes of spread (Charles et al., 2009; Petersen and Charles, 1997). Infected vines cannot be cured, so established vines have to be removed to stop the spread of GLR (Charles et al., 2010). Residence of GLR in the roots and soil around vines could limit the effectiveness of control, whether biological or chemical, and contribute to persistence after vine removal (Bell et al., 2009; Daane et al., 2012).

## 1.8 Current viticulture biological control

Supplementary planting has been shown to be successful in New Zealand vineyards for managing *E. postvittana* utilising a CBC protocol. *D. tasmanica* was the most ubiquitous parasitoid of *E. postvittana* which arrived in New Zealand from Australia (Charles et al., 1996; Suckling et al., 1998). *D. tasmanica* arrived incidentally with *E. postvittana* but this was followed later by a subsequent deliberate release (Suckling and Brockerhoff, 2010; Thomas, 1989). Through supplementary planting of buckwheat (*Fagopyrum esculentum* (Polygonaceae)), phacelia (*Phacelia tanacetifolia* (Hydrophyllaceae)) and alyssum (*Lobularia maritima* (Brassicaceae)), management of *E. postvittana* could be improved to reduce

the need for insecticides (Berndt et al., 2002; Berndt and Wratten, 2005; Berndt et al., 2006; Irvin et al., 2006; Scarratt et al., 2008). These plant species are cheap to sow and provide nectar that improves *D. tasmanica* fitness. However, the relationship between supplementary planting and effective *E. postvittana* larvae management was not always clear (Bell et al., 2006). Similar work has been done in Australia with *Trichogramma carverae* (Hymenoptera: Trichogrammatidae), an endemic parasitoid of *E. postvittana* (Begum et al., 2004, 2006; Gurr and Nicol, 2000).

While *D. tasmanica* was the predominant parasitoid observed utilising *E. postvittana* in New Zealand vineyards, a range of species have been identified as predators, and potential as biological control, including; the whirligig mite (*A. bacarrum*), spiders, European earwig (*Forficula auricularia* (Dermaptera: Forficulidae)), European harvestmen *Phalangium opilio* (Arachnida: Opiliones), and ladybird spp. (Coccinellidae) (Danthanarayana, 1983; Frank et al., 2007; Hogg et al., 2014; Paull et al., 2012).

No specific CBC management of mealybugs in New Zealand vineyards currently exists. With the decrease in broad spectrum insecticide use and more targeted use of "soft" chemical insect control, natural enemies have benefited (Charles et al., 2010; Charles, 1993; Daane et al., 2012). Utilising these natural enemies have become more important as sustainable production pressures have increased. Identifying suitable species that could be managed and incorporated as proven and quantifiable protocols for mealybug control (Charles et al., 2010).

There is potential for biological control through natural enemies that are already present in New Zealand vineyards. A 16 year survey of *Ps. calceolariae*

and *Ps. longispinus* in New Zealand by Charles et al. (2010) found parasitoids of six species of Encyrtidae, two Pteromalidae, and one Aphelinidae species. Four of these parasitoids were raised from both mealybug species; *Anagyrus fusciventris* (Hymenoptera: Encyrtidae), *Tetracnemoidea brevicornis* (Encyrtidae), *Ophelosia charlesi* (Hymenoptera: Pteromalidae), and *Coccophagus gurneyi* (Hymenoptera: Aphelinidae). Four predator species were observed; *Cryptolaemus montrouzieri* (Coleoptera: Coccinellidae), *Midas pygmaeus* (Coleoptera: Coccinellidae), *Diadiplosis koebelei* (Diptera: Cecidomyiidae), and *Cryptosceneia australiensis* (Neuroptera: Coniopterygidae). *D. koebelei* can account for predation of 30% of adult female *Ps. longispinus*, though are susceptible to broad spectrum insecticides (Charles, 1985). Encouragingly, these natural enemies appear to be present in most of New Zealand’s wine producing regions (Charles et al., 2010; Charles, 1993).

Supplementary plantings in vineyards increases habitat complexity to provide alternative prey and refuge for natural enemies, decreasing pest densities in adjacent vine rows (Altieri et al., 2005; Nicholls et al., 2008). This may be done with native plant species in New Zealand vineyards, not only providing a method to promote biological control but cultural and conservation benefits (Tompkins and Mason, 2008).

### 1.8.1 Pest management complementary to CBC

Judicious applications of specific insecticides when required can play a role in integrated pest management (IPM) programs, as the impact on natural enemies is minimised (Irvin et al., 2006; Varela et al., 2008). The change in vineyard pest management has generally been to use growth inhibitors such as tebufenozide (Confirm) and methoxyfenozide (Intrepid) for *E. postvittana*, and buprofezin for

mealybugs (Lo and Walker, 2011; Manktelow et al., 2005; Varela et al., 2008). These products are endorsed by SWNZ and can be included in pest control without losing accreditation (Fantail Viticulture Consultants, 2013).

Past introductions for classical biological control of *E. postvittana* and mealybugs have occurred. *Xanthopimpla rhopaloceros* (Hymenoptera: Ichneumonidae), *Glavidorsum stokesii* (Hymenoptera: Ichneumonidae), and *Trigonospila brevifacies* (Diptera: Tachinidae) are confirmed established parasitoids of *E. postvittana* that were released into New Zealand (Suckling and Brockerhoff, 2010; Thomas, 1989). A further release of 250 *D. tasmanica* were released in 1969 despite that the parasitoid was incidentally introduced earlier (Thomas, 1989). *C. gurneyi* was the only parasitoid deliberately introduced to control mealybugs, as was the predator *C. montrouzieri* (Daane et al., 2012). Additionally, there has been a subsequent release of *Pseudaphycus maculipennis* (Encyrtidae), a parasitoid of *Ps. viburni*.

IPM has particular relevance in regards to management of *E. postvittana*. This pest species has proved to be relatively phenotypically plastic which is a cause for concern because of the potential to adapt to new environments and resistance to pest control methods, including chemical insecticides (Suckling and Brockerhoff, 2010; Suckling et al., 1990). Coupled with the CBC method mentioned above, there exist other tools available to create an IPM regime (Suckling and Brockerhoff, 2010; Varela et al., 2008); using pheromone traps (Delate et al., 2008), mating disruption (Suckling et al., 1990; Suckling and Shaw, 1995), and management of under and between vine ground cover to remove plants that can encourage *E. postvittana* and promote natural enemies (Rogers et al., 2003; Suckling et al., 1998).

Limitations on grape production without organophosphates are particularly troublesome with cryptic and persistent pests. Systemic insecticides are effective against sucking pests such as mealybugs compared to contact foliar sprays (Lo and Walker, 2011). Improvement of mealybug detection is necessary as subterranean and under bark habitation can delay management and can inhibit removal (Daane et al., 2012; Lo and Walker, 2011). Research of sex pheromones will not only improve in pest detection, but can be incorporated into potential mating disruption or pheromone traps for both *Ps. calceolariae* (El-Sayed et al., 2010; Unelius et al., 2011) and *Ps. longispinus* (Millar et al., 2009; Waterworth et al., 2011). Development of CBC mealybug control with detection and trapping methods, can aid in limiting the spread of mealybugs and GLRaV-3 and decreasing their persistence in vineyards.

## 1.9 Aims

Theory and examples of the benefits and limitations of generalist predators have been discussed, and the potential of utilising assemblages of natural enemies with diverse modes of attack and habitat range. In a commercial setting where economic considerations are vital, conserving biodiversity for biodiversity's sake is not always justifiable. From the standpoint of the vineyard manager, identifying the more effective natural enemies and assemblages than broad stroke biodiversity conservation is attractive for the time and effort spent. Using theoretical and applied examples from the literature to determine aspects that require investigation, potential generalist insect predators will be identified for incorporation into CBC.

With an existing biological control protocol for *E. postvittana* that employs the parasitoid *D. tasmanica*, incorporating a complementary generalist predator may

have merit. In addition to augmenting *E. postvittana* management, there may be an additional benefit of inhibiting mealybugs as a vector of GLRaV-3. Candidates for controlling *E. postvittana*, generalist predators that consume mealybugs could be advantageous and perhaps develop a "broad-spectrum" biological control agent of two important vineyard pests. A likely generalist predator of these capabilities would aid in reducing two pest species responsible for a significant portion of insecticide use in New Zealand's vineyards.

The overarching aims of this thesis is therefore to identify which of the generalist invertebrate predator species within vineyards are suitable for complementing *D. tasmanica* in controlling *E. postvittana*, and will be addressed with the aims detailed in the following chapters:

## **Chapter 2**

1) Survey the predator diversity present in Marlborough vineyards; 2) which of the predator species present in the vineyards contribute to the removal of *E. postvittana* from vines; and 3) with organic and conventional vineyards available, an opportunity was presented to compare the influence of management on these first two objectives and additionally *E. postvittana* consumption rates.

## **Chapter 3**

For the generalist insect vineyard predators of *E. postvittana* identified in Chapter 1, laboratory experiments were run to: 1) ascertain maximum consumption rates of the primary pest species, *E. postvittana*; which of these predator species also consume the secondary pest *Ps. calceolariae*, and their maximum consumption rates; and comparisons are made between 3) predator species, and 4) prey species.



## Chapter 4

1) preferences of predators experiments were compared between *E. postvittana* larvae and eggs, and 2) between *E. postvittana* and *Ps. calceolariae* prey, to determine potential suitability of predators to manage a single or both pest species, field microcosms were used to incorporate the role of the habitat on foraging.

## Chapter 5

Utilising field cages again, 1) the influence of inter-specific interactions for each combination of predator species on consumption of *E. postvittana* and *Ps. calceolariae* prey were examined. Practical and theoretical examples have shown enhancing one or more predator species may impact on other predators of the same prey or a combination of predators may form an assemblage that improves pest management.

## Chapter 2

# Predation of *Epiphyas postvittana* eggs and larvae in Marlborough vineyards, New Zealand.

### Abstract

Interest in using generalist predators from within an ecosystem as part of conservation biological control (CBC) to manage pests has increased. To develop a CBC practice to control the vineyard pest *Epiphyas postvittana*, the range of predator species present in vineyards and those that predate upon the pest need to be identified. Ground and vineyard canopy surveys of the functional predator diversity were collected by beating and pitfall traps from six conventional and six organic vineyards in Marlborough, New Zealand. Collection of predators observed attacking larvae and eggs from sentinel bait cards in the vine canopies identified predators of *E. postvittana*. Comparisons of egg and larval predation between organic and

conventional vineyards were also made over 24 hours with sentinel bait cards. The mite *Anystis baccarum* was the species observed most frequently across vineyards attacking eggs (75% of sites) and larvae (75%), along with the harvestmen *Phalangium opilio* (8.3% eggs and 16.7% larvae) and the earwig *Forficula auricularia* (33% larvae) these were the only predator species observed. Functional predator diversity and the frequency of observations of predators attacking *E. postvittana* on bait cards were higher in organic vineyards yet the removal rates from bait cards did not differ between vineyard management types. Increased diversity in organic vineyards may have translated to increased predation if a wider range of prey species and consequent ecosystem services were included. These three generalist predator species were relatively common throughout vineyards. Further work is warranted with these predators to determine their suitability as CBC agents, particularly their impacts on other predator and prey species.

## 2.1 Introduction

The demand for sustainable primary production is increasing for commodities, including products such as wine (Bisson et al., 2002; Pretty and Bharucha, 2014; Tilman et al., 2011), which have discerning consumers that desire environmentally attractive products while remaining commercially competitive (Pimentel et al., 1992; Cullen et al., 2008; Forbes et al., 2011). Harnessing ecosystem services to manage pest species can assist sustainability and production, mitigating production and market pressures. Interest in maintaining biodiversity and the ecosystem services provided has increased, leading to research in this key area of production (Schneider and Brose, 2013; Geiger et al., 2010; Cardinale et al., 2012; Schmitz, 2009). To develop protocols which utilise the biodiversity of an ecosystem, it is vital to identify which species provide the desired ecosystem services and which

are most cost-effective in production systems.

Biological control is an ecosystem service that utilises biodiversity, but by simply measuring species diversity the ecosystem services provided may be overstated (Long and Finke, 2014; Finke and Snyder, 2008; Hooper et al., 2005; Tilman et al., 1997). Increased predator diversity has often been associated with improved biological control of pests (Schmitz, 2007; Sandhu et al., 2015; Sih et al., 1998). This improvement is often assumed to be due a greater range of predator species able to attack the pest, but potentially this can be independent of diversity but an artefact of the “identity effect”. This effect arises from the presence of more predator species increasing the probability that one species is a highly effective predator of the pest and increased predation, rather than the higher biodiversity predators in itself (Long and Finke, 2014; Loreau et al., 2001; Naeem, 1998). Organic management has often shown an increase in biodiversity within agricultural systems, though this is not always expressed as improved pest control (Sandhu et al., 2015; Macfadyen et al., 2009; Bengtsson et al., 2005; Zehnder et al., 2007). Ecological function is not necessarily tied to species diversity, but the diversity of functional traits (Schmitz, 2007; Thies et al., 2011). A more representative appraisal of ecosystem services provided by predator species is given by quantifying functional diversity rather than solely measuring predator species diversity, though functional and species diversity are invariably connected (Hooper et al., 2005; Thies et al., 2011; Loreau et al., 2001; Tilman et al., 1997).

The diversity of functional traits is seen to be a better indicator of ecosystem services over species richness. Generally, mode of hunting or habitat range are important considerations, along with taxonomy and morphology, when determining the functional trait of a predator species (Petchey and Gaston, 2002; Schmitz,

2007; Wright et al., 2006). Two different species can overlap in habitat use and mode of hunting or, different life stages of a single predator species can have divergent functional traits (Sih et al., 1998; Petchey and Gaston, 2002). Functional diversity is founded on groups of species which share taxonomic, physiological, ecological, or morphological traits that contribute to a function within an ecosystem (Tilman, 2001; Petchey and Gaston, 2002; Wright et al., 2006; Schmitz and Sokol-Hessner, 2002). Maintenance of functional diversity and diversity within functional groups can improve resilience against disruption by natural or anthropogenic disturbances to ecosystem services provided by predators, the “insurance hypothesis” of biodiversity (Tscharntke et al., 2005; Bengtsson et al., 2003; Loreau et al., 2003; Macfadyen et al., 2009). The functional diversity is relative to the context and extent of the spatial or ecosystem service of concern, and the abiotic and biotic parameters specific to this ecosystem (Schmitz, 2007; Petchey and Gaston, 2002; Hooper et al., 2005).

To begin building the case for using generalist invertebrate predators as conservation biological control (CBC) agents, it is essential to know what predator species are already present within the vine ecosystem, and which of these predate on *Epiphyas postvittana* (Lepidoptera: Tortricidae). The vineyards used (see below) provide an opportunity to examine possible consequences of organically and conventionally managed vineyards on functional predator diversity and predation of *E. postvittana*. This study surveyed the existing invertebrate predator community and those that have potential as CBC agents to complement an existing biological control agent, *Dolichogenidea tasmanica* (Hymenoptera: Braconidae). The parasitoid *D. tasmanica* is a CBC agent of *E. postvittana* in New Zealand vineyards (Scarratt et al., 2008; Berndt et al., 2002, 2006).

Three main objectives were investigated in this chapter to determine the potential for using generalist invertebrate predators as biological control agents of *E. postvittana* in vineyards: 1) ascertain the functional invertebrate predator diversity in both organically and conventionally managed vineyards; 2) identification of the predator species that contribute to the removal of *E. postvittana* from vines with direct observation to remove the need to infer relationships from correlations of predator and pest presence, so pest consumption could be expressly attributed to predator species; 3) determine relative field consumption rates of *E. postvittana* by predators in vineyards, to identify if existing vineyard management influences with pest consumption.

## **2.2 Methods**

### **2.2.1 Field site**

#### **Marlborough**

New Zealand's largest wine-producing region, Marlborough, is situated at the north-east corner of the South Island. All fieldwork was undertaken at Wither Hills Ltd vineyards on the southern Wairau Plain. This plain comprises deep alluvial free-draining river beds covered with mid-low fertility soils that are stony with a shallow sand loam horizon (Robinson et al., 2006; Caspari et al., 1997; Bramley et al., 2011). Annual mean sunshine for the province is 2500 h and there are approximately 650-700 mm mean annual rainfall (Caspari et al., 1997; Jacometti et al., 2007).

#### **Vineyards**

All vineyards used in this work were located within 4 kilometres of the Wither Hills Ltd winery. The three most widely grown varieties in New Zealand, Pinot Noir, Sauvignon Blanc and Chardonnay, were used for this work. Six vineyards in conversion to certified organic status (BioGro<sup>™</sup> New Zealand Ltd) were selected for this study; two Pinot Noir, two Sauvignon Blanc, and two Chardonnay. These vineyards had been organically managed for less than three years, the minimum required for organic BioGro<sup>™</sup> New Zealand Ltd certification, but are referred to as organic or organically managed for the rest of this chapter. Each of these six organic vineyards was paired with one conventionally managed vineyard of the same variety less than one kilometre apart and on similar soil type that was compliant with Sustainable Winegrowing New Zealand<sup>®</sup>.

### **2.2.2 Experimental protocol**

The first season of sampling was done between October 2010 to April 2011, but methodology was revised in February 2011 to that described below, as sampling had previously focused on spider species. Sampling after March was disrupted by grape harvest so after this date it was discontinued. This methodology was repeated in February and March in 2012 but due to logistical issues, not all three sampling methods were completed in March. Only data from February of 2011 and 2012 were used in the analysis as these were the only months that all methods were repeated in both seasons. This period closest to harvest is when damage by leafrollers is most pronounced (Lo and Murrell, 2000).

### **Functional predator diversity**

Functional predator diversity was measured in each vineyard to gauge the potential effective biodiversity (Uetz et al., 1999; Luck et al., 2003; Hooper et al., 2005). Stratified sampling of terrestrial and vine canopy predators was done once per month in each of the twelve vineyard blocks by pitfall trapping and beating, as using a single method can bias the species sampled (Topping and Sunderland, 1992). Sampling specifically targeting invertebrates in flight was not done because of the proximity of some vineyards of both management types.

- Pitfall traps were set under vines on the outermost row and in the row closest to 40 m from the edge, with two traps in each row, separated by at least 30 m. Metal sleeves were dug into the ground and cups with 80 mm openings (100 mm deep) were placed inside so that the rim was flush with the ground. Monopropylene glycol 80% was poured inside the cup 20 mm deep as a preservative. These traps had metal covers 5 cm above the cup rim



to stop rain and debris entering the cup (Topping and Sunderland, 1992). Traps were set for 48h periods and contents emptied at the end of this time.

- Vines were beaten for 30 seconds then predators that had fallen on to a 1 m x 1 m catching cloth were collected with an aspirator. This method was repeated at nine randomly selected sites no closer than 30 m within each vineyard block. Beating was done using a modified method from Costello and Daane (2005), using a smaller catching cloth than the 9 m<sup>2</sup> cloth but repeated to have the equivalent total area. Beating was done once during the same period as pitfall traps were set in the morning between 05:00 h and 10:30 h.

Specimens were placed in 95% ethanol and brought to the laboratory for identification and classified into functional groupings by family or genus that related to the species hunting strategy as the measure of functional diversity; spiders were assigned to functional groups described in Uetz et al. (1999), such orb-weavers or ground-runners. All juvenile spiders were removed from the analysis as species could not always be identified, so could not be assigned to a functional group as spiders have a relatively diverse range of functional traits between each genus (Uetz et al., 1999). Identification was not as specific for other functional groups as either: only a single species was identified for a taxonomic group, or the method of predation did not vary greatly within a taxon. To give definitive functional groupings, detailed micro-habitat and hunting mode use by predators is required for the range of predator species collected (Wright et al., 2006; Loreau et al., 2001). Detailing behaviour and ecology of a range of species is a problematic task, which was logistically impractical during this study so taxonomy was as a proxy to define functional groups where necessary (Hooper et al., 2005; Soluk, 1993).

### **Predators of *E. postvittana***

To identify the predators of *E. postvittana* in vineyards of different management types, a similar method to Pfannenstiel and Yeargan (2002) of using baited cards placed in the field was used. The two types of bait cards used comprised either *E. postvittana* eggs or larvae. Egg masses were bought as waxed paper sheets on which *E. postvittana* had laid them and third-instar larvae were provided in containers with diet, sourced from New Zealand Institute for Plant & Food Research Ltd, Auckland.

Area of egg masses were measured by overlaying the partially opaque wax proof paper sheets over a black and white 1 mm<sup>2</sup> grid. Sheets were cut into clusters of 30 mm<sup>2</sup> ( $\pm 5$  mm<sup>2</sup>) without damaging eggs by cutting between egg masses. Six larvae were stuck onto filter paper by spraying aerosol adhesive glue (Selleys® Kwik Grip Spray) evenly across the paper. Once the surface was tacky, 6.5-7.5 mm long larvae were scattered on the filter paper. The end of the abdomens were gently pushed down with a soft fine paintbrush to fix the larvae onto the paper; this enabled the larvae to still move without leaving the bait card. The number of larvae and area of egg masses on bait cards were decided on after preliminary trials which gauged approximate maximum consumption rates in the time period.

Both bait card types were placed in each of the twelve vineyards at a similar arrangement as the pitfall trap layout (see above), with two survey points on the outer row and two on a row 40 m from the vineyard edge. One of each bait type was put at each point at approximately 1.35 m high and they were separated by 2 m. Cards were stapled to the abaxial surface of vine leaves and a small square of white insulation tape was stuck to the adaxial surfaces so bait cards could be quickly found at night without disturbing the predators. Cards were placed in

the vineyards between 18:00 and 20:00, then revisited every 3 h for a 24h period starting at 21:00. If a card was completely depleted it would be refreshed with a new bait card on the same leaf. Any predators seen on the cards were put in 95% ethanol and labelled by: location, time, and bait type, then identified to species later.

### ***E. postvittana* removal rates**

A comparative removal rate of *E. postvittana* larvae and eggs without disturbance to predators was measured with bait cards similar to those used in the previous trial. The number of larvae was increased from six to eight per card, and the area of egg masses per card from 30 to 40 mm<sup>2</sup> ( $\pm 2$  mm<sup>2</sup>) in this trial to ensure that cards were not depleted, as they could not be replaced during the trial. Due to more of both bait types being used per card, and supply constraints, the number of cards was reduced to two of each bait card type per vineyard. With fewer bait cards, the arrangement was also modified in each vineyard to: one survey point on the outside row, and one point on the row closest to 40 m from the vineyard edge. Starting at 18:00, bait cards were attached to leaves and marked with insulation tape as above for 24h, with the number of prey remaining on the cards were counted.

### **2.2.3 Analysis**

For analysis of functional predator diversity, a repeated measures ANOVA (R Development Core Team, 2011) was used with vineyard management and vine cultivar as factors over 2011 and 2012 to compare the diversity between vineyards.

Observations of predators consuming *E. postvittana* on bait cards were transformed into presence-absence data for each predator species in each vineyard, due to high variability of the number of observations for predator species at each vineyard. The presence-absence data gave a frequency of which predator species observed consuming *E. postvittana* across the vineyards. Both *E. postvittana* larvae and egg bait cards were used in the same analysis, with prey type as a factor. A generalized linear model was constructed with binary data with a logit link to the main factor (VSN International, 2011). Five factors: management, cultivar, predator species, prey type and year were used in the analysis, with only pair-wise interactions examined for parsimony.

*E. postvittana* removal rate data were analysed with a repeated-measures ANOVA (R Development Core Team, 2011) in a similar manner to the functional predator diversity, with vineyard management and vine cultivar as factors over 2011 and 2012. The proportion of larvae consumed from a bait card was arcsine transformed to convert the binomial percentage data to a normal distribution. Separate analyses were done for the *E. postvittana* larvae bait cards and egg bait cards.

## 2.3 Results

Functional predator diversity was higher in organically managed vineyards that were in conversion from conventional management to certified BioGro™ New Zealand organic, than in conventionally managed vineyards ( $F = 13.44$ ,  $p = 0.011$ ) (Figure 2.1). Season and vine variety did not significantly affect diversity of predator functional groups. The most abundant functional group in ground and canopy surveys was predatory mites (56.9%), followed by *Phalangium opilio* (Arachnida: Opiliones) (14.2%), ground-running spiders (Lycosidae and Dysderidae) (12.4%), coccenellids (7.2%), and *Forficula auricularia* (Dermaptera: Forficulidae) (5.1%) (Table 2.1).

Functional group	Conventional				Organic			
	2011	2012	Total	%	2011	2012	Total	%
Carabid	0	1	1	0.1	2	0	2	0.2
Chilopoda	1	1	2	0.2	3	8	11	1.1
Coccenellid	14	4	18	1.8	43	10	53	5.4
<i>F. auricularia</i>	19	12	31	3.2	11	8	19	1.9
<i>P. opilio</i>	14	31	45	4.6	56	39	95	9.7
Predatory mite	59	102	161	16.4	67	332	399	40.5
Spider GR	26	19	45	4.6	51	26	77	7.8
Spider OW	2	0	2	0.2	0	1	1	0.1
Spider ST	1	0	1	0.1	1	0	1	0.1
Spider WS	5	1	6	0.6	6	1	7	0.7
Staphylinid	2	0	2	0.2	4	1	5	0.5

Table 2.1: Total predators of all six vineyards surveyed of conventional and organic management for each functional predatory group and year of surveying. The sums of invertebrate predators for each vineyard were pooled from pitfall trapping and canopy beating. Percentage values are the number of predators in each functional group from either vineyard management type of the total number of predators caught. Spider species fell within four functional groups (GR = ground runners, OW = orb weavers, ST = Stalkers, WS = Wandering sheet builders) (Uetz et al., 1999).

Only three predator species were observed consuming either *E. postvittana*

larvae or eggs over both seasons; *Anystis baccharum* (Prostigmata: Anystidae), *F. auricularia*, and *P. opilio*. There was a significant difference in the proportion of sites that predators species were observed predating on bait cards ( $p < 0.001$ ) (Figure 2.2). This was largely due to *A. baccharum* being present at 75% of sites on both bait card types. *F. auricularia* was observed at 33% of sites on larvae bait cards and were not observed consuming any *E. postvittana* eggs. *P. opilio* was only at 8.3% and 16.7% of sites on egg and larvae bait cards respectively. The significant interaction between predator species and bait type ( $p = 0.008$ ) could be attributed to *F. auricularia* consuming only *E. postvittana* larvae in this trial (Figure 2.2).

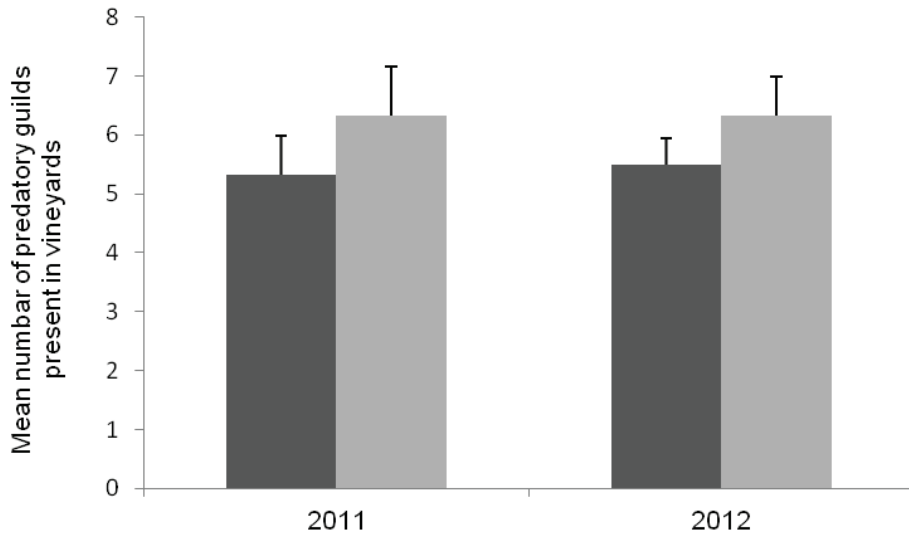


Figure 2.1: Mean number of functional predatory groups (95% CI) observed by pitfall trapping and vine beating in conventionally managed vineyards ( $n = 6$ ) (dark) and vineyards in organic conversion ( $n = 6$ ) (light) in 2011 and 2012.

Organic vineyards had more observations of predators consuming *E. postvittana* from bait cards than those that were managed conventionally ( $p = 0.046$ ). This result appears to have been driven predominantly by observations of *A. bac-*

larvae or eggs over both seasons; *Anystis baccharum* (Prostigmata: Anystidae), *F. auricularia*, and *P. opilio*. There was a significant difference in the proportion of sites that predators species were observed predating on bait cards ( $p < 0.001$ ) (Figure 2.2). This was largely due to *A. baccharum* being present at 75% of sites on both bait card types. *F. auricularia* was observed at 33% of sites on larvae bait cards and were not observed consuming any *E. postvittana* eggs. *P. opilio* was only at 8.3% and 16.7% of sites on egg and larvae bait cards respectively. The significant interaction between predator species and bait type ( $p = 0.008$ ) could be attributed to *F. auricularia* consuming only *E. postvittana* larvae in this trial (Figure 2.2).

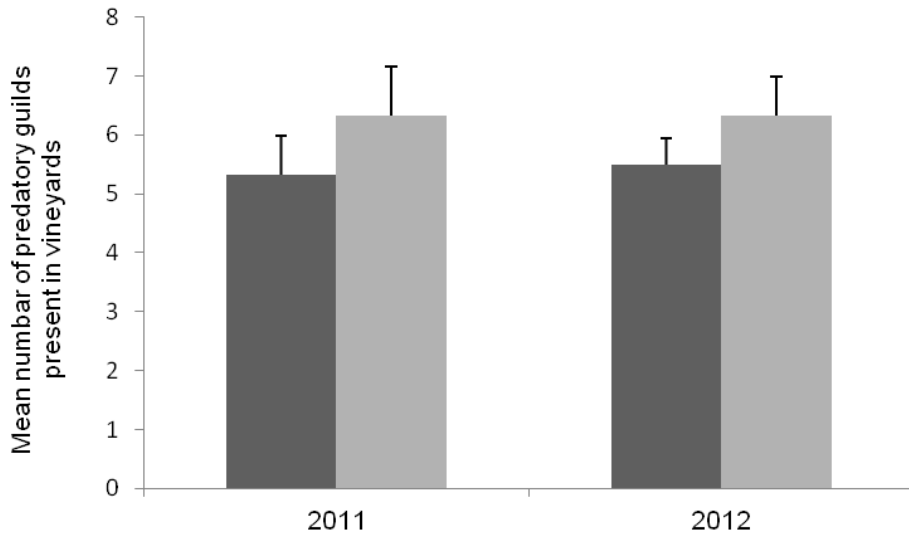


Figure 2.1: Mean number of functional predatory groups (95% CI) observed by pitfall trapping and vine beating in conventionally managed vineyards ( $n = 6$ ) (dark) and vineyards in organic conversion ( $n = 6$ ) (light) in 2011 and 2012.

Organic vineyards had more observations of predators consuming *E. postvittana* from bait cards than those that were managed conventionally ( $p = 0.046$ ). This result appears to have been driven predominantly by observations of *A. bac-*

*carum*, with little difference between *F. auricularia* and *P. opilio* across management types (Figure 2.3). However, the interaction between management type and predator species was not significant ( $p = 0.113$ ). No other interactions between management type and other factors were significant, either.

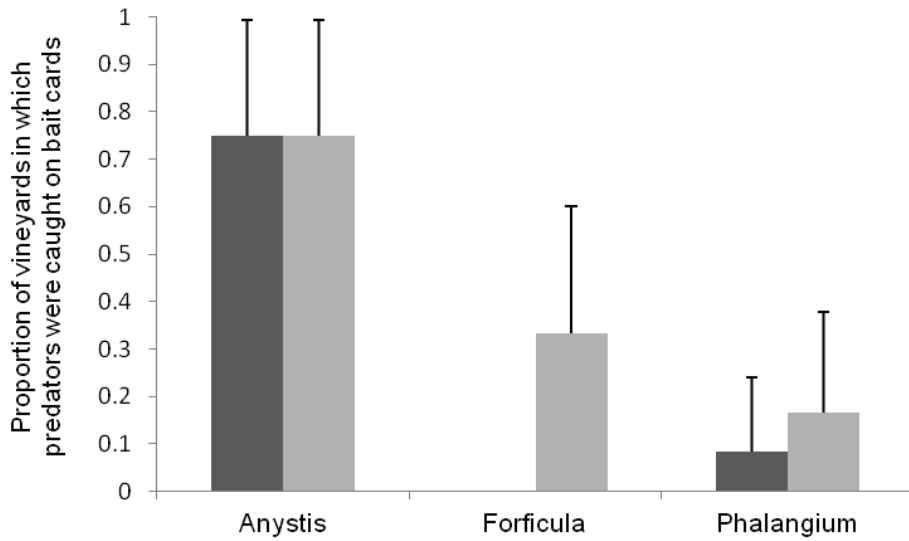


Figure 2.2: Proportion of vineyards each predator species (95% CI) were observed and collected from bait cards of *E. postvittana* eggs (dark) ( $n = 12$ ) and *E. postvittana* larvae (light) ( $n = 12$ ).

The changes between predator species found on bait cards in successive seasons were significant ( $p < 0.001$ ), possibly due to the increase of *A. baccharum* observations and absence of *P. opilio* in the 2012 season (Figure 2.4). *F. auricularia* was present in similar proportions of sites over both years (Figure 2.4).

No clear relationships occurred between *E. postvittana* consumption rates and seasons (Figure 2.5) or vineyard management (Figure 2.6). The potentially higher predation rate of *E. postvittana* larvae in conventionally managed vineyards ( $\bar{x} = 0.63$ ) than in organic vineyards ( $\bar{x} = 0.52$ ) was not significant ( $F = 3.81$ ,  $p =$



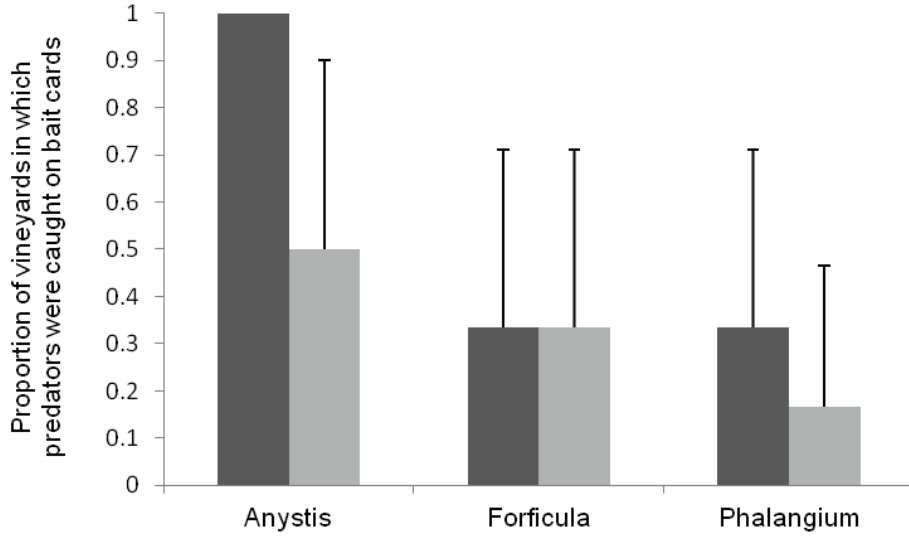


Figure 2.3: Proportion of vineyards on which each predator species (95% CI) were observed and collected from bait cards of *E. postvittana* eggs and *E. postvittana* larvae in vineyards in organic conversion (dark) and conventionally managed vineyards (light).

0.099). The interaction between the vineyard management type and season was also not significant ( $F = 4.58$ ,  $p = 0.076$ ), despite the possible drop in larvae predation in the 2012 season (Figure 2.5). Area of *E. postvittana* egg masses removed was potentially higher in organic vineyards ( $\bar{x} = 6.13 \text{ mm}^2$ ) than in conventional vineyards ( $\bar{x} = 0.85 \text{ mm}^2$ ) (Figure 2.6) though this difference was also not quite significant ( $F = 5.44$ ,  $p = 0.058$ ).

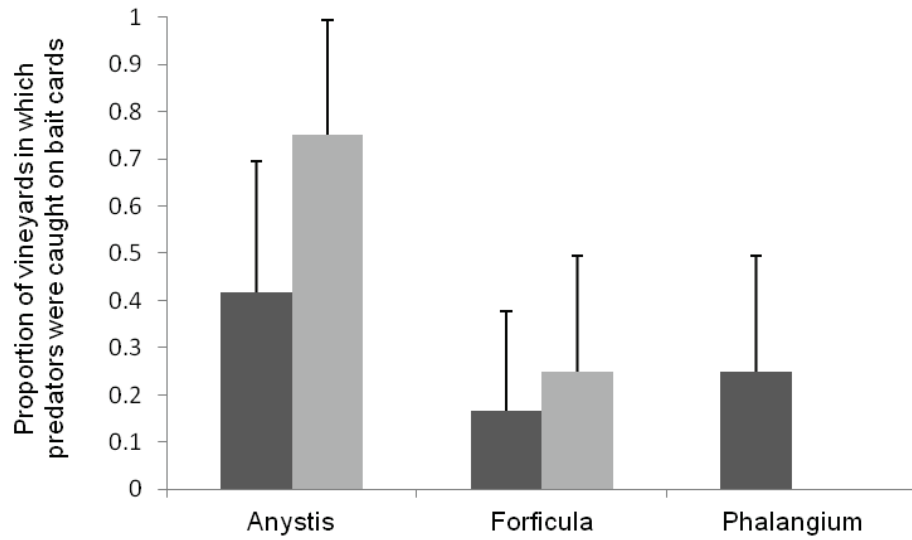


Figure 2.4: Proportion of vineyards each predator species (95% CI) observed and collected from bait cards of *E. postvittana* eggs and *E. postvittana* larvae in vineyards in 2011 (dark) (n = 12) and 2012 (light) (n = 12).

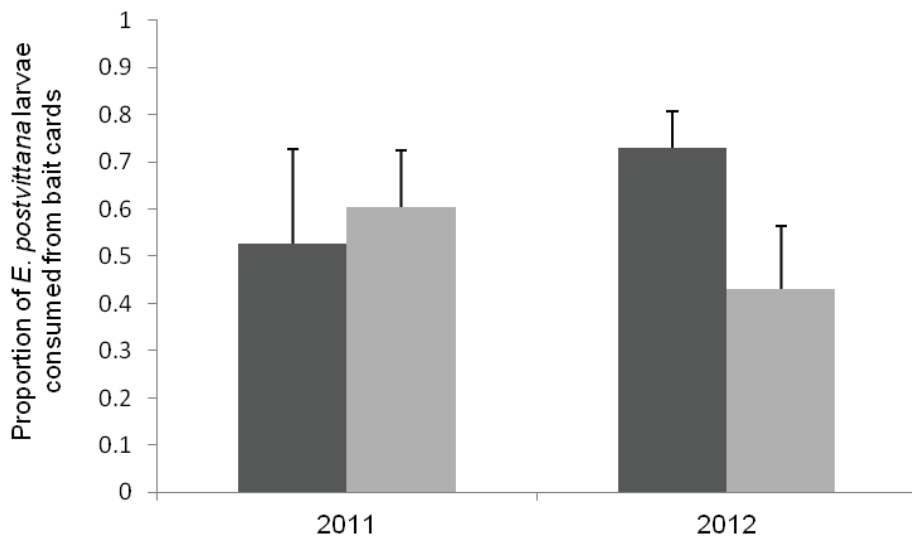


Figure 2.5: Proportion of *E. postvittana* larvae consumed (95% CI) from bait cards in conventionally managed vineyards (dark) (n = 6) and vineyards in organic conversion (light) (n = 6) in the 2011 and 2012 harvest seasons.

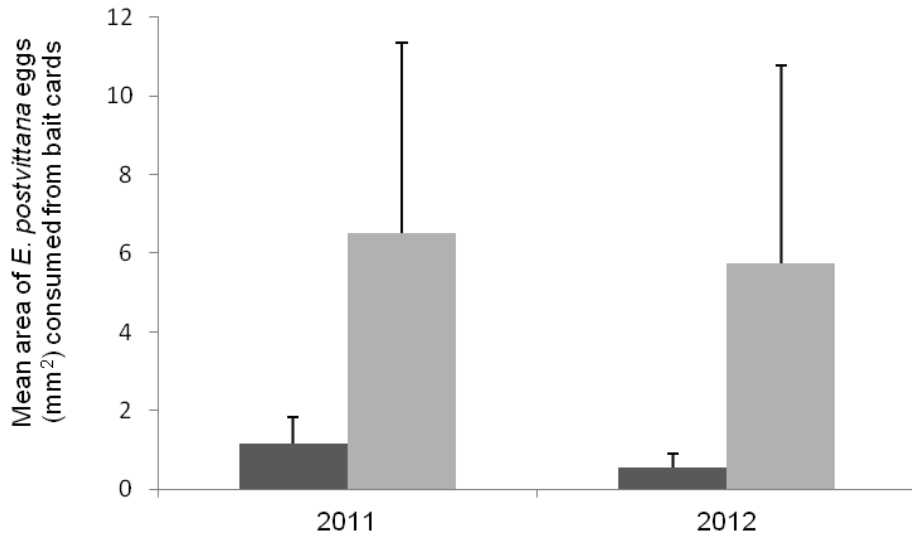


Figure 2.6: Mean consumption rate of *E. postvittana* egg mass area ( $\text{mm}^2$ ) from bait cards (95% CI) in conventionally managed vineyards (dark) ( $n = 6$ ) and vineyards in organic conversion (light) ( $n = 6$ ) in the 2011 and 2012 harvest seasons.

## 2.4 Discussion

CBC relies on identifying and engaging potential biological control agents that are already present in an ecosystem. To investigate the suitability of generalist invertebrate predators as CBC agents of *E. postvittana*, it was necessary to establish what predator species are present and which of those predated on this pest species. Consumption rates of the immature forms of the *E. postvittana*, and how the management of the vineyard influenced the predator diversity composition and their impact on *E. postvittana* were the aspects of vineyard ecology examined. Organic vineyard management and season appeared to influence predator diversity and the activity of predators consuming *E. postvittana*. The consumption of the baits used in the vineyard can be attributed largely to *A. baccarum*, *F. auricularia* and *P. opilio* from the observations made in this study. Not all predation events would have been observed, so infrequent predators of *E. postvittana* or predator

species at low density were less likely to have been detected.

Organic vineyard management correlated with increased functional predator diversity. Theoretical studies and examples of higher functional diversity presumably leading to decreased pest damage have previously been presented (Schmitz, 2007; Pretty and Bharucha, 2014; Long and Finke, 2014), and can also benefit the resilience of ecosystem service delivery to disturbances (Hooper et al., 2005; Symondson et al., 2002). The organically managed vineyards used in this study were within three years of conventional management ceasing and not yet certified organic, indicating a relatively short-term benefit for functional predator diversity. Increased habitat heterogeneity is often correlated with higher predator diversity and more effective pest control (Östman et al., 2001; Geiger et al., 2010; Macfadyen et al., 2009). Decreased vineyard disturbance by removing some conventional vine management methods, such as chemical inputs, can improve habitat heterogeneity and may account for the increased functional predator diversity (Landis et al., 2000; Gibson et al., 2007; Winqvist et al., 2011).

However, there were no clear patterns of *E. postvittana* consumption rates being higher in organic vineyards, as there was with functional predator diversity. This suggests “redundancy” in the predator diversity or that the diversity does not translate into higher *E. postvittana* predation. This study only considered predation of one species, whereas the sampling of functional diversity had a wider scope, and all three predator species observed predating on *E. postvittana* were wide-spread. The nature and number of species interactions within and between functional groups would need examination to further understand the ecosystem services operating here, stable provision of ecosystem services and the impact on pest populations (Straub et al., 2008; Thies et al., 2011; Dunne et al., 2002). A

study that includes a wider range of pest species may find that the higher functional diversity observed may correlate with predation of multiple pest species and other ecosystem services.

There is potential for all three predators *A. baccarum*, *F. auricularia* and *P. opilio*, to be used as biological control agents of this pest. *A. baccarum* was the most widely observed predator across vineyards for both bait types regardless of season, vineyard management and vine cultivar. During this study *F. auricularia* was observed attacking *E. postvittana* in more vineyards than *P. opilio* but the former predator was seen consuming only larval baits, despite occasional sightings of them eating eggs during preliminary trials [pers. obs.]. Understanding the cause of the observed seasonal variation of predator species feeding at the bait cards may indicate pathways to promote them as pest management tools. Employing a multi-predator species biological control method could mitigate seasonal effects and disturbance (Straub et al., 2008; Hooper et al., 2005).

Sampling during this study was not a comprehensive survey of all predator species, the biggest gap in collection was targeting flying predators and only some species were collected. This highly mobile assemblage was disregarded not because of a lack of prospective application as biological control agents, but the focus on non-flying predators was to examine relatively less transient populations in the perennial vineyard environment (Symondson et al., 2002; Thies et al., 2011). However, flying predators have potential as their greater dispersal ability could compensate for the lower fecundity of generalist predators compared to specialists or parasitoids (Symondson et al., 2002; Thies et al., 2011).

Together, *A. baccarum*, *F. auricularia* and *P. opilio* accounted for all observations of predators consuming *E. postvittana* from bait cards. This work builds on previous work by Frank et al. (2007) and Anderson (2012) who observed, with video, *F. auricularia* eating *E. postvittana* larvae in the canopy of New Zealand vineyards, and Anderson (2012) also observed larval predation by *P. opilio*. *F. auricularia* has been shown to feed on *E. postvittana* in other studies (Danthanarayana, 1983; Suckling et al., 2006; Tompkins and Mason, 2008), as has *A. baccarum* (Paull et al., 2012; Baker, 1983), and *P. opilio* (Danthanarayana, 1983). Each of these predators have also previously shown other potential as a biological control agent (Schmaedick and Shelton, 2000; Suckling et al., 2006; Mueller et al., 1988; Moerkens et al., 2011; Cuthbertson and Murchie, 2005, 2004).

By periodically sampling predators consuming *E. postvittana* from bait cards over 24 h, only “snapshots” of predation events were obtained. This method identifies the predominant predators but is unlikely to include those that are infrequent and opportunistic or are at low densities in the vineyards. Employing contemporary techniques, such as molecular gut and stable isotope analyses (Lefort et al., 2012; Boyer et al., 2012; Symondson and Harwood, 2014), could help to identify predators through analysing trapped and collected predators to detect those missed by direct observations of predation.

Three species of generalist predators have been identified that may contribute to the control of *E. postvittana* and complement *D. tasmanica*. Identifying how and to what extent *A. baccarum*, *F. auricularia* and *P. opilio* interact to improve or inhibit predation on the pest population will be a necessary step in understanding the potential of these generalists as biological control agents. The extent and nature of the predator species interactions with other beneficial and pest species

within the ecosystem need to be understood to improve the development an applicable management tool. Parameters of their ability to predate on *E. postvittana*, and how they interact with other predator species, prey species and the vineyard habitat are key factors for future research.

## Chapter 3

# Consumption rates of *Epiphyas postvittana* and *Pseudococcus calceolariae* by the generalist predators *Anystis baccarum*, *Forficula auricularia* and *Phalangium opilio*

### Abstract

Three generalist invertebrate predator species, *Anystis baccarum*, *Forficula auricularia* and *Phalangium opilio*, were shown to be widespread in vineyards and they were predators of the pest *Epiphyas postvittana*. The broad diet of these potential biological control agents may aid in management of a second important vineyard



pest, the mealybug *Pseudococcus calceolariae*. Consumption rate trials were carried out in laboratory conditions in simple Petri dish arenas to remove influences of habitat and inter- and intra-specific interactions to observe the species' maximum potential predation over 24 hours. Wild caught predators were presented with either *Ps. calceolariae* nymphs, adult female *Ps. calceolariae*, *E. postvittana* egg masses or larvae. There was no significant difference in consumption rates between the sexes of adult *F. auricularia* and *P. opilio* across prey types. *F. auricularia* was the only species to predate on adult female *Ps. calceolariae* and it killed more *Ps. calceolariae* nymphs, *E. postvittana* eggs and larvae than the other predator species. *E. postvittana* eggs was the only prey type *A. baccharum* predated on, at a consumption rate not significantly different from *P. opilio*. *F. auricularia* and *P. opilio* displayed potential as biological control agents of both pest species, with *F. auricularia* the most voracious across the widest range of prey types. However, *A. baccharum* may still play a role in improving *E. postvittana* pest management, despite being limited in the prey types that it attacked.

### 3.1 Introduction

Generalist predator species interact directly with more species within an ecosystem by consuming a range of species, competing with other predators to utilise these prey species, and the habitats they occupy (Nilsson, 2001; Straub et al., 2008; Snyder and Wise, 1999). Though, in relatively less diverse modified habitats, such as agricultural systems, the range of interactions of generalists can become restricted (Rosenheim et al., 1993). There may be potential to use this wider connectance to suppress a secondary pest species (Symondson et al., 2002; Tylianakis and Romo, 2010). The examination of a generalist predators' interaction with a specific prey species can be difficult to isolate in the field. The generalists' breadth of diet and varying levels of polyphagy, often across trophic levels, can make understand-

ing the predators effects difficult (Symondson et al., 2002; Rosenheim et al., 1993).

This thesis focuses on assessing the potential of generalist predators to reduce direct and indirect vine damage caused by *Epiphyas postvittana* (Lepidoptera: Tortricidae) and *Pseudococcus calceolariae* (Hemiptera: Pseudococcidae). In Chapter 2, three generalist predator species were observed consuming *E. postvittana*; these were *Anystis baccarum* (Prostigmata: Anystidae), *Forficula auricularia* (Dermaptera: Forficulidae) and *Phalangium opilio* (Arachnida: Opiliones). The relative predation rates of *E. postvittana* eggs and larvae between vineyards were examined in Chapter 2, though not what proportion *A. baccarum*, *F. auricularia*, and *P. opilio* contributed to this consumption. Predation by these predators may complement the parasitoid *Dolichogenidea tasmanica* (Hymenoptera: Braconidae) (Paull et al., 2012; Cardinale et al., 2003) which has been utilised to manage *E. postvittana* in New Zealand vineyards (Scarratt et al., 2008; Berndt et al., 2002, 2006).

All three predator species are generalists, so the importance of *E. postvittana* in their diet may vary; also these predators may differ in the extent to which they attack different life stages of the pest species (Riechert and Bishop, 1990; Tylianakis and Romo, 2010). Ascertaining the maximum consumption rates of the predator species demonstrates potential in isolation from other factors that influence predation rate; e.g., prey density, search effort, prey choice, intra-guild competition and predation, and habitat complexity (Abrams, 1993; Nilsson, 2001; Landis et al., 2000; Jonsson et al., 2008). This baseline information is useful for designing future experiments where the influence of factors on foraging can be observed through variation from the maximum consumption rate.

In the following work, direct predator-prey species interactions were isolated

in laboratory experiments to remove influences that affect consumption that are present in the field. Consumption rates of the same *E. postvittana* life stages as used in Chapter 2 (third instar larvae and eggs) plus *Ps. calceolariae* nymphs and adult females were evaluated. The four objectives of this experiment were: 1) establish predator species' maximum consumption rates of the primary pest species, *E. postvittana*; 2) identify which of the generalist predators of *E. postvittana* in vineyards also consume a secondary pest, *Ps. calceolariae*, and their maximum consumption rates; 3) determine the differences between the predator species in utilising different developmental stages of the pest species; and 4) compare pest consumption rates between predator species.

## 3.2 Methods

### 3.2.1 Arthropods used

#### Predator species

*A. baccarum* was caught in the Lincoln University vineyard by beating the vine canopy and capturing large specimens that fell on to the beating tray. Determining age and sex of mites was difficult while alive because specimens were wild caught, this could not be done accurately without harm. Of every group of 30 large individuals caught, the largest ten, judged by eye, were taken to the controlled environment room for consumption-rate trials of each prey type.

*F. auricularia* were caught from a peach orchard (*Prunus persica* (L.) Batsch var. *persica*) at the organic Biological Husbandry Unit (BHU), Lincoln University ([www.bhu.org.nz](http://www.bhu.org.nz)). Strips of corrugated cardboard, approximately 200 mm wide, were wrapped around the branches of the trees with the corrugated side against the bark and stapled to hold the resulting tube in place. These shelters were opened when required above a collection tray and ten adults of each sex were used for consumption rate trials of each prey type. The adult stage was determined by the presence of hind wings, and the sex of specimens by the shape of their cerci (Rankin and Palmer, 2009).

*P. opilio* was collected by hand from areas of long rank grasses around the BHU. Ten each of male and female specimens were used in each round of consumption rate trials; only adult specimens (body length  $\geq 5.5$  mms) were used (Edgar, 1966), a crude but less harmful method of selecting adults. Males were identified by their "horns", an enlarged apophysis on the chelicerae (Allard and

Yeargan, 2005)

### **Prey species**

Both prey species, *E. postvittana* and *Ps. calceolariae*, came from laboratory cultures at the New Zealand Institute for Plant & Food Research Ltd, Auckland. Prior to experiments they were stored or cultured within controlled environment room (see "Consumption rate trials" below) so they were acclimatised for the trials.

*E. postvittana* eggs and larvae were ordered fortnightly to maintain a stock of 7.5-8.5 mm larvae and of unhatched eggs. Larvae were kept in plastic lunch boxes (200 x 120 x 80 mm) with holes in the lid covered by porous paper. Larval length was measured immediately prior to the consumption trial beginning; handling was with a damp, fine paint brush.

Egg masses were laid on sheets of waxed paper and these were cut into smaller pieces. The area of egg masses was measured by overlaying the pieces of paper onto a black and white chequered 1 mm<sup>2</sup> grid and measuring the area covered by egg masses with a microscope. Any masses with darkened eggs were discarded so no larvae would hatch during the 24 h period experiment.

Six separate *Ps. calceolariae* cultures were started from ten infested potatoes. Each culture was kept in the controlled environment room within plastic lunch boxes (200 x 120 x 80 mms), with a bed of vermiculite to maintain humidity and a fine mesh panel on the lid to permit ventilation. Mealybugs were raised on seed potatoes (*Solanum tuberosum* cv. Désirée). Potatoes were replaced as they

began to age and shrivel. *Ps. calceolariae* was removed from those potatoes with a damp, soft, fine paint brush.

### 3.2.2 Experimental protocol

Arenas were created with 50 mm Petri dishes with a damp dental cotton roll to maintain humidity and were sealed with Parafilm. Preliminary trials and main experiments were done between October 2011 and January 2012. All invertebrate cultures and experiments were in controlled environment rooms (18 °C ( $\pm 2$  °C), 16 h light: 8 h dark). After adults of each predator species were caught from the grounds of Lincoln University, New Zealand, 48 h starvation period began after capture in Petri dishes with the same layout as the arenas.

Each trial gave a single predator 24 h to consume one prey type of either 7.5 - 8.5 mm *E. postvittana* larvae, *E. postvittana* egg masses, adult female *Ps. calceolariae* >5 mm, or 2 - 2.5 mm *Ps. calceolariae* nymphs. The quantity of prey given varied between predator species (Table 3.1); quantities were greater than maximum consumption observed in preliminary trials. Prey were placed into arenas immediately prior to the introduction of predators and the experiments then began.

	<i>E. postvittana</i>		<i>Ps. calceolariae</i>	
	larvae	eggs (mm <sup>2</sup> )	adult females	nymphs
<i>A. baccharum</i>	5	100	2	2
<i>F. auricularia</i>	10	200	10	10
<i>P. opilio</i>	20	100	5	8

Table 3.1: Quantities of *E. postvittana* and *Ps. calceolariae* prey given to the predators *A. baccharum*, *F. auricularia* and *P. opilio* in arenas over a 24 h period.

### **3.2.3 Analysis**

Consumption rates of each prey type were analysed for an effect of predator type by the Kruskal-Wallis test with Minitab Statistical Software v.15 (Minitab Inc., State College, Pennsylvania, USA). This non-parametric test ranks values and does not assume normal distribution or equal variance. For analyses that showed a significant effect of predator species on consumption rates of a prey type, there was further analysis with the Mann-Whitney U test, another non-parametric test. This test compares each pairing of predator species within a prey type experiment, to identify which of the predator species were significantly different from the others.

### 3.3 Results

In Kruskal-Wallis tests for consumption of each prey type, there was a significant effect of predator species on rankings of consumption rate ( $p \leq 0.000$ , adjusted for ties, for all prey types). All prey consumption tests were analysed further with the Mann-Whitney U test where possible, to identify which predator species were responsible for these significant results. Where there were no observations of a predator species consuming a prey type, the Mann-Whitney U test could not be carried out. *A. baccharum* did not consume any *Ps. calceolariae* prey or medium sized *E. postvittana* larvae and *P. opilio* did not consume adult female *P. calceolariae*. Both sexes of *F. auricularia* had an average rank higher than the overall median rank for every prey type ( $Z > 0$ , Table 3.1) whereas, the average rank for *A. baccharum* and both sexes of *P. opilio* was lower than the overall median ranking for each prey type ( $Z < 0$ , Table 3.2). These relationships suggest that *F. auricularia*, the largest predator involved, could be largely attributed for the patterns observed between predator treatments.

Further analysis with the Mann-Whitney U test showed no significant difference between sexes of *F. auricularia* ( $p > 0.05$ , adjusted for ties, for all tests) nor for *P. opilio* ( $p > 0.05$ , adjusted for ties, for all tests except adult female *Ps. calceolariae*) (Figures 3.1, 3.2, 3.3, and 3.4). As indicated in Table 3.1, *F. auricularia* had a significantly higher consumption rate than did other predators of *Ps. calceolariae* nymphs, *E. postvittana* eggs and larvae ( $p < 0.000$ , adjusted for ties for all prey types,  $\bar{x} = 5.4$ ,  $\bar{x} = 92.3\text{mm}^2$ , and  $\bar{x} = 15.4$ , respectively) (Figures 3.1, 3.2, 3.3, and 3.4), though comparisons could not be made where predators did not consume any prey. Only *F. auricularia* was able to consume adult female *Ps. calceolariae* ( $\bar{x} = 7.2$ ,  $\bar{x} = 6.9$ ; female and male, respectively) (Figure 3.3).



Species/sex	<i>E. postvittana</i> larvae				<i>E. postvittana</i> eggs				<i>Ps. calceolariae</i> adults				<i>Ps. calceolariae</i> nymphs			
	N	Median	Ave.	Z	N	Median	Ave.	Z	N	Median	Ave.	Z	N	Median	Ave.	Z
<i>A. baccharum</i>	10	0.000	5.5	-4.85	10	3.000	18.3	-1.76	10	0.000	15.5	-2.43	10	0.000	7.0	-4.49
Female <i>F. auricularia</i>	10	15.000	39.9	3.48	103.500	42.3	4.06	5.000	42.1	4.04	7.000	41.6	3.92			
Male <i>F. auricularia</i>	10	15.500	41.1	3.80	81.000	38.8	3.21	4.500	38.9	3.24	7.000	39.4	3.36			
Female <i>P. opilio</i>	10	3.500	21.1	-1.06	0.000	14.4	-2.69	0.000	15.5	-2.43	1.500	20.0	-1.33			
Male <i>P. opilio</i>	10	3.500	19.9	-1.37	0.000	13.9	-2.83	0.000	15.5	-2.43	2.000	19.5	-1.46			

Table 3.2: Results of Kruskal-Wallis test of laboratory consumption rates by the generalist predators *A. baccharum*, *F. auricularia* and *P. opilio* of viticultural pests *E. postvittana* and *Ps. calceolariae*.

There was no significant difference in *E. postvittana* egg consumption (Figure 3.2) between *A. baccharum* ( $\bar{x} = 3.5$ ) and *P. opilio* ( $\bar{x} = 5.1$ ,  $p = 0.397$ ; and  $\bar{x} = 5.6$ ,  $p = 0.231$ , adjusted for ties; female and male *P. opilio* respectively). *P. opilio* consumed *E. postvittana* larvae (Figure 3.1) and *Ps. calceolariae* nymphs (Figure 3.4) when there were no observations of predation by *A. baccharum*. Some *E. postvittana* larvae did form silken refuges at the edges of the Petri dishes, though this defence was limited by the immediate introduction of the predators after larvae were placed in the arenas.

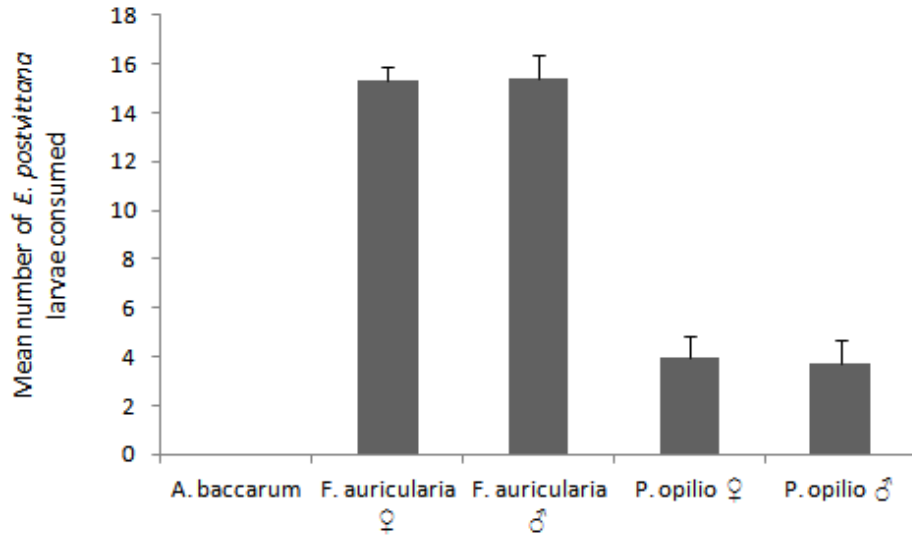


Figure 3.1: Number of *E. postvittana* larvae (95% CI) consumed by *A. baccharum*, female and male *F. auricularia*, and female and male *P. opilio* in a 24 hour period within an arena after a 48 hour starvation period.

Despite observations of *A. baccharum* feeding on *E. postvittana* larvae (7.5 - 8.5 mm) in vineyards (Chapter 2), there was no consumption of the same sized larvae within the arenas (Figure 3.1). An additional trial was carried out with *A. baccharum* and 10 first instar *E. postvittana* larvae (< two days old), using the same protocol as other trials in this chapter, to test if the lack of previously

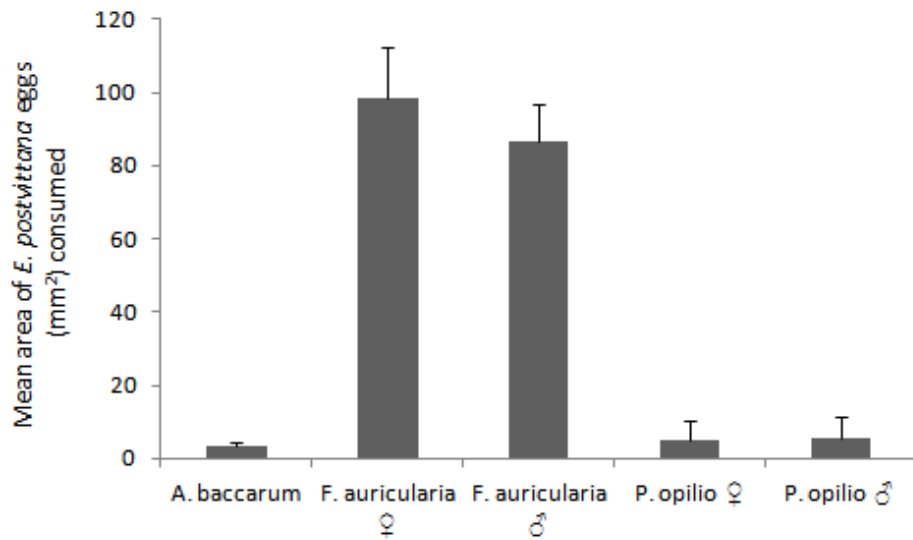


Figure 3.2: Area of *E. postvittana* eggs (mm<sup>2</sup>) (95% CI) consumed by *A. baccharum*, female and male *F. auricularia*, and female and male *P. opilio* in a 24 hour period within an arena after a 48 hour starvation period.

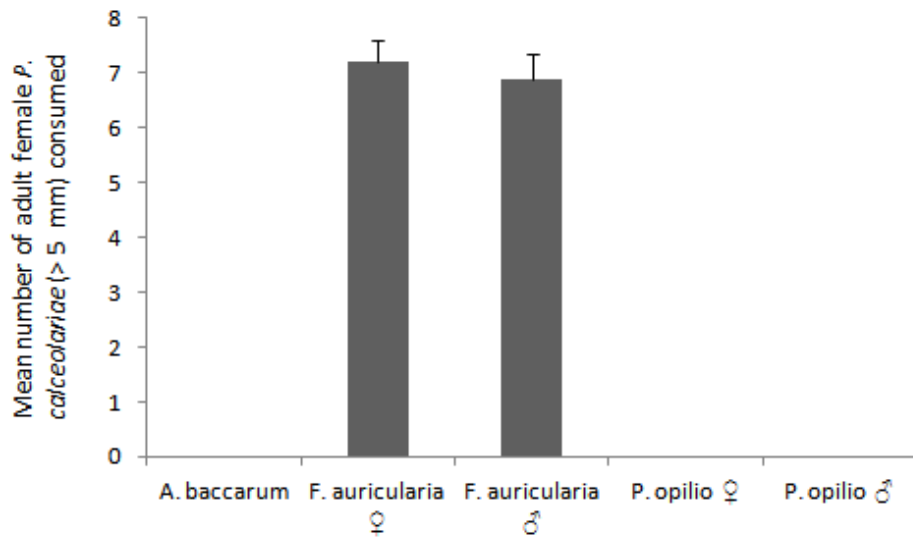


Figure 3.3: Number of adult female *Ps. calceolariae* (95% CI) consumed by *A. baccharum*, female and male *F. auricularia*, and female and male *P. opilio* in a 24 hour period within an arena after a 48 hour starvation period.

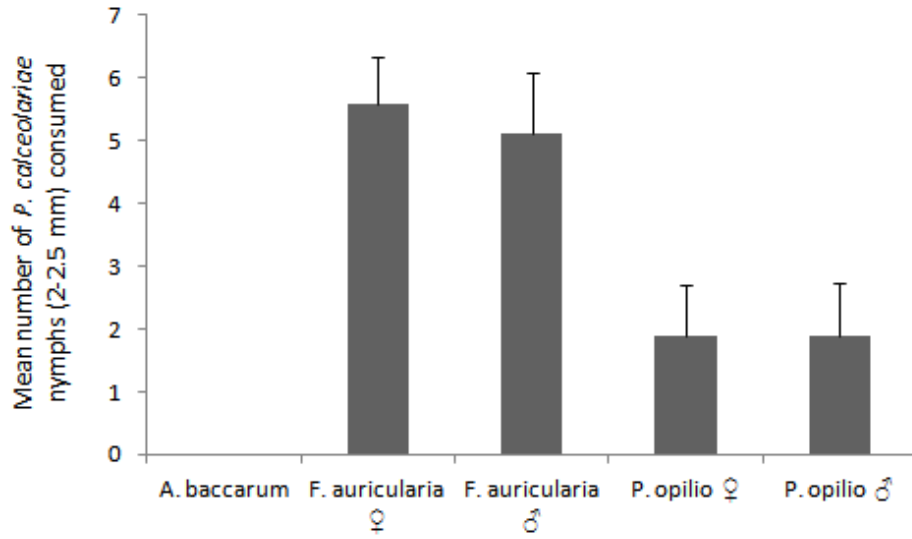


Figure 3.4: Number of *Ps. calceolariae* nymphs (2 - 2.5 mms) (95% CI) consumed by *A. baccharum* (n=10), female and male *F. auricularia*, and female and male *P. opilio* in a 24 hour period within an arena after a 48 hour starvation period.

observed consumption in these arenas was due to; an inability to kill or feed on medium sized larvae, or a lack of inclination. First instar *E. postvittana* larvae were consumed by *A. baccharum* ( $\bar{x} = 7.78, \pm 0.025, 95\% \text{ CI}$ ), showing an ability and inclination to consume *E. postvittana* larvae but a limitation of successfully predating on larger larvae.

### 3.4 Discussion

Predator-prey and parasitoid-host interactions are a cornerstone of ecology, and biological control seeks to enhance the effectiveness of the third trophic level in productive systems (Eber, 2001; Gurr et al., 2003; Rosenheim et al., 1993; Gurr et al., 2012). However, isolating the contribution of a single predator or parasitoid species can be complex in open ecosystems (Long and Finke, 2014). Predation can potentially be used to complement the biological control delivered by the parasitoid *D. tasmanica* with predators identified in Chapter 2 (Scarratt et al., 2008; Berndt et al., 2002, 2006). Search effort, predator density, inter/intra predator species interactions, and habitat complexity were removed through the experimental design, to isolate the maximum potential consumption rate.

*F. auricularia* consumed all prey types and the most of each prey type per individual, highlighting this species as a potential biological control agent, not only of the primary vineyard pest of this study, *E. postvittana*, but also of *Ps. calceolariae*. *P. opilio* consumed both pest species though not the adult female *Ps. calceolariae* prey. *P. opilio* consumed less of all prey types in comparison to *F. auricularia*, and *E. postvittana* egg consumption was similar to the much smaller *A. baccharum*. While *A. baccharum* consumed only *E. postvittana* eggs and first instar larvae, they may still have a role in reducing the populations of the primary pest and therefore complementary to existing vineyard management of *E. postvittana* with *D. tasmanica* or the larger generalist predators.

The larger mass of *F. auricularia* would largely account for the higher consumption of both *E. postvittana* larvae and eggs than *P. opilio* and *A. baccharum*. Physiological differences such as palatability and nutritional benefit derived from prey may also play a role in consumption rates between the predator species

(Singer, 2000). The defences of *E. postvittana* and *Ps. calceolariae* may differ in effectiveness between predator species.

*P. opilio* was observed consuming both pest species within the limited arenas of these experiments, as well as *E. postvittana* in field observations (see Chapter 2). There was no difference in consumption rates of *E. postvittana* eggs between *P. opilio* and the smaller *A. baccharum*. The lack of predation by *P. opilio* of larger *Ps. calceolariae* could be due to the ostiolar fluid or the waxy secretions excreted by *Ps. calceolariae* being an effective anti-predator defence in this situation (Daane et al., 2008).

The smaller size of *A. baccharum* coupled with the tortricid larval defence of vigorous wriggling to avoid predation and parasitism is a probable cause of the lack of larval consumption in this experiment (Rosenheim et al., 1993). Previous studies (Paull et al., 2012; Baker, 1983), field observations (see Chapter 2) and the additional trial with first instar larvae in this experiment showed a proclivity and ability of *A. baccharum* to feed on *E. postvittana* larvae; though movement of medium sized larvae was inhibited in Chapter 2. *A. baccharum* were not able to consume *Ps. calceolariae* and were limited in the size of *E. postvittana* larvae they are able to attack, there is still potential for this generalist predator to be used as an effective biological control agent. *A. baccharum* have been highlighted as a predator of a variety of other pest species (Ridsdill-Smith, 1997; Cuthbertson and Murchie, 2003; Cuthbertson et al., 2003) and could provide an indirect benefit to pest management.

An avenue worthy of investigation is to consider facilitative relationships between predators. Using *Balaustium* species (Acari: Erythraeidae) as mite preda-

tors of *Calliphora stygia* (Diptera: Calliphoridae), Merfield (Merfield et al., 2004) found a four-fold increase in egg predation by *P. opilio* when eggs were pierced by mites. Predation was even higher when eggs were manually pierced. While this study used a different mite predator and prey species, it is plausible that parallel relationships with *E. postvittana* eggs could occur. There may be potential to use *A. baccharum* to improve *E. postvittana* egg predation by facilitating *P. opilio*. To pursue this line of research it is necessary to examine how pest predation is affected when these two species interact as well as potential enhancement techniques for one or both species.

Laurin and Bostanian (2007) commented that *A. baccharum* is rapacious, feeding on any prey they can subdue, and in Chapter 2 this predator were observed attacking restrained third-instar *E. postvittana* larvae. This provides another possibility for an indirect contribution to pest mortality. Disturbance of larger larvae by predators that they cannot kill themselves, can make them prone to other predators that able to (Losey and Denno, 1998). *A. baccharum* was not able to disturb *E. postvittana* larvae within their silken leaf rolls (Paull et al., 2012), though larvae outside leaf rolls may be disturbed by *A. baccharum*, inducing an anti-predator behaviour that makes the larvae prone to predation by other species.

While *F. auricularia* and *P. opilio* consumed both prey species, prey preference could alter consumption rates outside these no-choice laboratory trials. Recent molecular developments in diet analysis provide new tools that could help to garner a more complete picture of the diet of *F. auricularia*, *A. baccharum* and *P. opilio*. While *A. baccharum* was not able to consume medium sized *E. postvittana* larvae or *Ps. calceolariae* in the limited and simple laboratory conditions, there may be some synergies with other predators or habitat that make these pests prone in a

more open system (Paull et al., 2012; Schmitz, 2007; Sih et al., 1998). Isotope analysis and molecular gut analysis are two analytical tools of diet that could improve the understanding of alternative prey species (Wise et al., 2006; Cuthbertson et al., 2003; Harwood et al., 2008; Boyer et al., 2012; Lefort et al., 2012).

The maximum potential consumption rates are an indication of predator capability, not a realistic consumption rate, as predators are often in some degree of starvation (Symondson et al., 2002) and influenced by foraging trade-off behaviour (Persons, 1999; MacArthur and Pianka, 1966; Charnov, 1976). The predator-prey relationships examined in this chapter would need to progressed via experiments within heterogenous habitats that include wider community influences. A predators community relationships are not limited to the prey the consume, the inter-predator species interactions were excluded within the trials in this chapter. An assemblage of predator species can complement or hinder predation of a pest species through facilitation, antagonism and intra-guild predation (Sih et al., 1998; Straub et al., 2008; Schmitz, 2007). Understanding how these generalist predators affect each other is an important step in developing a quantifiable biological control agent. Additionally, it is necessary to examine the inter-specific relationships *in situ*. Making predictions across eco-types and differing taxonomic scales within a trophic systems does not always translate which alters how various ecosystems responds to manipulation, particularly terrestrial invertebrate systems (Vance-Chalcraft et al., 2007).

This basic examination of the direct interactions between predators and pest species provides an initial building block for future work in this vein. Three inter-specific aspects of foraging behaviour have been highlighted for further investigation in the work in this chapter:



1) predators' prey preference, if the pest species these predators have been shown to consume are preferred in the field or if search effort increases as pest density increases;

2) inter- and intra-specific predator interactions, is there a beneficial, neutral, or negative effect on pest predation when multiple predator species are present; and

3) the predator-prey interactions, identifying the range of prey of these three predators in vineyards.

This work has built on Chapter 2 to discern how much *E. postvittana* the three predators can consume and that *F. auricularia* and *P. opilio* could also consume a secondary pest, *Ps. calceolariae*. The experimental design limited predators to only one prey type requiring no search effort and therefore do not represent what could be reasonably expected to be observed in a field setting, but gives a maximum potential consumption and provides a useful tool for designing future experiments.

## Chapter 4

# Prey choice by the generalist predators *Forficula auricularia* and *Phalangium opilio* on the viticultural pests *Epiphyas postvittana* and *Pseudococcus calceolariae*.

### Abstract

As conservation biological control (CBC) becomes more attractive in production systems and generalists predators are engaged to control pests, additional benefits to pest management may arise. Two predators, *Forficula auricularia* and *Phalangium opilio*, were observed attacking the pest *Epiphyas postvittana* in vine-

yards and a second vineyard pest *Pseudococcus calceolariae* in the laboratory, presenting a possible opportunity to manage multiple pest species. Predators were presented with individual or pair-wise combinations of *Ps. calceolariae* nymphs, *E. postvittana* egg masses and larvae in vine canopy cages, and consumption rates of prey over 24 hours were recorded. Analysis of consumption rates incorporated predator electivity and prey acceptability when testing for preference. The sole preference displayed by either predator species was *P. opilio* having preference for *E. postvittana* eggs over larvae, with 47.7% more eggs eaten and 48.7% fewer larvae than predicted. When presented with a single prey type, *F. auricularia* predated on 51.6% more *Ps. calceolariae* nymphs and 57.3% more *E. postvittana* larvae than *P. opilio*, but there was no significant difference between predator species with *E. postvittana* eggs. A lack of preference does not limit these species' ability as vineyard pest management tools as prey selection between prey species was frequency-dependent. The preference of *E. postvittana* eggs over larvae by *P. opilio* may enhance complementary pest management with the larval parasitoid *Dolichogenidea tasmanica*.

## 4.1 Introduction

Crucial to identifying the suitability of a predator or parasitoid as a biological agent, whether classical, augmentative or conservation biological control, is the nature of the relationship and frequency of interactions between potential agent and the pest species (Louda et al., 2003; Bale et al., 2008; Symondson et al., 2002). In the case of classical and augmentative biological control, which predominantly introduce specialist natural enemies into an ecosystem (Bale et al., 2008; Zehnder et al., 2007), pest specificity to limit unintended impacts is desired and necessary (Louda et al., 2003; Snyder and Wise, 1999; Chang and Kareiva, 1999). Generalist predator species' diminished reliance on the target pest can improve population

stability throughout the year by feeding on alternative prey species in times of food scarcity, a potential benefit in conservation biological control (CBC) setting by improving early season predation (Symondson et al., 2002; Settle et al., 1996; Chang and Kareiva, 1999).

Understanding the relationship natural enemies and pest is necessary in order to apply a successful biological control protocol, which is further complicated with generalist predators as they inherently have more interactions with multiple prey species. The prey preference of generalist predator species' is important in determining suitability as a biological control application (Louda et al., 2003; Symondson et al., 2002). Prey preference is defined as a predator species characteristic, a behavioural response of the predator, a non-random association based on observations of prey consumption with and without choice where the observed consumption differs from the predicted (Underwood and Clarke, 2006; Jackson and Underwood, 2007; Singer, 2000; Rapport and Turner, 1970).

Two important concepts to incorporate when investigating if predation is in proportion to abundance or a preference occurs is acceptability and electivity. Acceptability is a characteristic of the prey species in relation to the predator species; this can alter if a characteristic of the prey species changes (Underwood et al., 2004; Singer, 2000). This could be manifested as changes in anti-predator behaviour or prey palatability. Electivity incorporates factors involved in the interaction between species, whereas the prey preference and acceptability are characteristics of the species interacting (Singer, 2000). Electivity can be altered by changes in species dispersion, density and search effort that influence the encounter rate, or time taken to catch and consume prey (Underwood et al., 2004; Jackson and Underwood, 2007; Rapport and Turner, 1970). If predation is randomly associ-

ated with prey (frequency-dependent), then prey is consumed in proportion to its abundance when electivity and acceptability are accounted for (Underwood et al., 2004).

In conjunction with investigating the potential of generalist invertebrate predators to complement *Dolichogenidea tasmanica* (Hymenoptera: Braconidae) in management of *Epiphyas postvittana* (Lepidoptera: Tortricidae), an objective of this study was to investigate the possibility of using generalist predators to manage multiple pests. Employing the wider diet of generalists for an additional pest management benefit. *Forficula auricularia* (Dermaptera: Forficulidae) and *Phalangium opilio* (Arachnida: Opiliones) were identified as two of the three principal predators of *E. postvittana* larvae and eggs in Marlborough vineyards (Chapter 2) and as predators of a secondary pest, *Pseudococcus calceolariae* (Hemiptera: Pseudococcidae) (Chapter 3). Establishing the relative prey preferences for *E. postvittana* and *Ps. calceolariae* by *F. auricularia* and *P. opilio* helps to clarify the potential for these generalist predators to be able to manage multiple pests.

Prey preference may not necessarily be commonplace in natural settings as limited availability of food removes choice (Symondson et al., 2002), but preference displayed in these experimental conditions can indicate what predator behaviour may occur. Non-random associations between predator and pest species are not always desired in a biological control setting. Randomly associated predation opens the possibility of prey switching and aggregation towards pest irruptions of both pest species (Symondson et al., 2002). The degree of divergence in habitat use and foraging behaviour by predators and parasitoids of the same species can affect the extent of enhancement or interference of pest mortality (Schmitz, 2007). A lack of preference by a generalist predator can help to mediate overlaps of prey or host

use with specialist control agents (Hogg et al., 2013; Colfer and Rosenheim, 2001). A strong preference for *E. postvittana* over *Ps. calceolariae* may limit the predator species implementation as a management tool of both pest species. Conversely, if the predators which were the most frequently observed taking *E. postvittana* in vineyards prefer *Ps. calceolariae*, then *Ps. calceolariae* may be eaten over and above the primary pest in this study.

This chapter builds on the previous ones to examine if *F. auricularia* and *P. opilio* display preferences for *Ps. calceolariae* nymphs, *E. postvittana* larvae or *E. postvittana* eggs. Adult female *Ps. calceolariae* were not used in this chapter as *F. auricularia* was the only predator observed consuming them (Chapter 3). Using the experimental design described in Underwood and Clarke (2005), acceptability and electivity can be taken into account to assess the prey preference of both predator species. Preferences, or lack of them, help to identify the prospects of these generalist predators as management tools of multiple pests or if the natural enemies are more appropriate for controlling a single pest. Comparisons of preference between *E. postvittana* larvae and eggs were also made.

## 4.2 Methods

### 4.2.1 Field site

Cossars Vineyard was used for prey preference trials, situated south of Christchurch, New Zealand, between the Halswell River and the Port Hills, near Tai Tapu, 9.5 km from Lincoln University. In the 2011-2012 summer growing season, vineyard management was limited to maintaining appearance for a neighbouring hospitality venture. The only cultivar used was Chardonnay, and all vine rows used in this experiment were in one vineyard block.

### Experimental cages

BugDorm<sup>™</sup> tube shaped cages (MegaView Science Co., Ltd., Taichung, Taiwan) were 700 mm long x 300 mm diameter (41 x 37 mesh/10 mm<sup>2</sup>) with each end cinched tight around the cane by a draw cord. In the centre of the cage there was a clear plastic band for viewing and a zip ran the length of the cage so that the tube could be opened to lie flat. To ensure no insect could enter or leave, a plastic cable tie was pulled tight over the ends of the cage next to the draw cord.

The leaves on canes were trimmed so that six remained with a total spread of less than 500 mm to standardise the arena complexity and area, and so cages could fit over canes comfortably. These cages restricted predator and prey dispersal while still containing aspects of the vine canopy habitat complexity. This was to include acceptability and electivity created by the habitat in the experiment (Underwood et al., 2004; Underwood and Clarke, 2005). Pyrethrum (Yates<sup>®</sup>, Nature's Way Pyrethrum) was sprayed thoroughly on to each cane prior to the cage being secured to ensure other invertebrates were removed. Arenas were left for at

least 48 hours before experiments commenced, to exceed the 24 hour withholding period of the pyrethrum treatment so invertebrates involved in experiments were unaffected.

#### **4.2.2 Arthropods used**

##### **Predator species**

*F. auricularia* and *P. opilio* were collected as described in Chapter 3, from the organic Biological Husbandry Unit (BHU), Lincoln University ([www.bhu.org.nz](http://www.bhu.org.nz)). Sex of predators were not considered as no significant difference was observed between sexes in consumption rates in laboratory experiments (Chapter 3). One individual predator was used per arena so consumption rates would not be influenced by intra-specific and inter-predator interactions.

*F. auricularia* was collected from a peach orchard (*Prunus persica* var. *persica*) at the BHU. Strips of corrugated cardboard, approximately 200 mm wide, were wrapped around the branches of the trees with the corrugated side against the bark and stapled to hold the resulting tube in place. These shelters were opened above a collection tray and adults were identified by the presence of hind wings extending past the tegmina. *P. opilio* was collected by hand from riparian strips and areas of long rank grasses around the BHU; only adult specimens (body length  $\geq 5$  mms) were used.

##### **Prey species**

Three different prey types were used; *E. postvittana* larvae (7.5 - 8.5 mm long), *E. postvittana* egg masses, and *Ps. calceolariae* nymphs (2 - 2.5 mm). Prey were



supplied by the New Zealand Institute for Plant & Food Research Ltd, Auckland. The prey types used in the experiment were those consumed by both predator species in Chapter 3.

Six prey treatments were used for each predator species; three treatments were of one prey type with no choice available, and three treatments of one of each pairwise combination of the three prey types. The same acceptability and electivity was included in no-choice treatments so prey preference by the predator species when choice was available could be identified.

Quantities of each prey type were in excess of the maximum amount consumed in preliminary trials so the prey could not be thoroughly depleted, and minimising any shift in electivity. The same number of *E. postvittana* larvae and *Ps. calceolariae* nymphs were released into cages so the initial densities were similar. Differing quantities of prey were presented to *F. auricularia* and *P. opilio* based on preliminary trial consumption. For *F. auricularia*, 14 larvae or nymphs were released in each the arena when required for the respective treatment, and 11 prey items for *P. opilio*.

*E. postvittana* egg masses arrived laid on sheets of waxed paper which were cut into smaller pieces. The area of each piece was measured to the nearest  $\text{mm}^2$  and the target area for treatments was made up from four pieces of paper with egg masses. Four of the six leaves within a cage had egg masses attached. These were stapled to the abaxial surface of separate leaves in the arena. *F. auricularia* and *P. opilio* were given  $80 \text{ mm}^2$  and  $45 \text{ mm}^2$  total egg masses respectively per treatment. Egg masses with existing damage were excluded from trials to ensure predators were not attracted by cues from damaged eggs and that any damage could be

clearly attributed to predators. *E. postvittana* egg masses are clumped and not able to disperse, unlike the other prey types, so egg masses were dispersed in cages across the leaves as widely as practicable to mitigate this issue. The eggs were not placed on the upper side of leaves to minimise dessication (Danthanarayana, 1983).

#### 4.2.3 Experimental protocol

Trials examining *F. auricularia* and *P. opilio* prey choice were run concurrently from February to April 2012. After capture, predators were starved in individual Petri dishes with damp dental rolls for 48 hours in a controlled environment (18 °C ( $\pm 2$  °C), 16 h light: 8 h dark). Prey items were measured and sorted in the laboratory prior to leaving for the vineyard. The appropriate prey types were released into randomly assigned cages, then were left to acclimatise and disperse throughout the arena for 24 hours before predators were introduced.

The trials ran for 24 hours from the time predators were introduced into the cages. After this period, the cages remained closed but the cane was cut from the vine and taken back to the laboratory. Arenas were opened separately and laid out flat so no specimens could hide in folds of the cage, and care was taken to ensure nothing escaped. Predators were collected first as they were more mobile and placed individually into labelled vials of high grade ethanol. Each leaf was removed and searched thoroughly for prey items then discarded, followed by the vine cane. The number of live *E. postvittana* larvae and *Ps. calceolariae* nymphs remaining, as well as the area of remaining undamaged *E. postvittana* egg masses in each arena were all recorded.

#### 4.2.4 Analysis

Using the analysis of preference of two prey types described in Underwood and Clarke (2005), the consumption of each two-way combination of the three prey types was examined for both predator species. The mean proportion of each of the two prey types consumed where the predator has no choice (Stage 1) were used to develop a predicted consumption rate, that included electivity and acceptability, when the choice of both prey types were presented the predator (Stage 2) (Underwood et al., 2004; Underwood and Clarke, 2005). Variance of observed prey consumption at Stage 2 from the predicted indicates prey preference by predator species.

Using the proportions of observed consumption by predators Stage 1 of prey A ( $m_a/M_a$ ) and prey B ( $m_b/M_b$ ) and Stage 2 ( $n_a/N$ ,  $n_b/N$ ), a non-naïve (accurate) estimation of Stage 1 consumption for prey A ( $p_a$ ) and B ( $p_b$ ) was calculated from maximal likelihood equations to account for Type 1 error (Underwood and Clarke, 2005; Underwood et al., 2004). The accurate estimations used data from Stage 1 and 2 observations to account for acceptability of the prey and electivity of the interaction. Using the calculated accurate estimations of Stage 1 ( $p_a$ ,  $p_b$ ), predicted proportions of random associated consumption for both prey types ( $q_a$  and  $q_b$ ) in Stage 2 were made. A null hypothesis was derived for each two-way prey choice for each predator with the estimated proportions:

$$H_0: q_a = \theta p_a; q_b = \theta p_b$$

The comparison to test the null hypotheses was made with  $\chi^2$  tests. The number of choices of prey types ( $k$ ) defines the degrees of freedom ( $k - 1$ ) (Jackson and Underwood, 2007). As separate individuals were used in each cage, the necessary

independence was fulfilled.

The rates of consumption of each of the three prey types with no alternative prey available were compared between the two predator species with a Students t-test with two-tailed samples of equal variance. This comparison helps to create a clearer of notion how the consumption rates of the predators change from laboratory trials (Chapter 3) to field cages in vineyards.

### 4.3 Results

*F. auricularia* showed no preference between *Ps. calceolariae* nymphs, *E. postvittana* larvae or *E. postvittana* egg masses. In all two-way comparisons of *F. auricularia* prey preference for the three bait types, there was no observed consumption that significantly differed ( $p > 0.05$ ) from the estimated proportional consumption (Table 4.1). Predation was random and proportional to prey abundance when accounting for electivity and prey acceptability.

		Treatment 1		Treatment 2		Treatment 3	
		<i>P. c.</i>	<i>E. p.</i>	<i>P. c.</i>	<i>E. p.</i>	<i>E. p.</i>	<i>E. p.</i>
		nymphs	larvae	nymphs	eggs	larvae	eggs
Stage 1	Observed	7.111	9.889	7.111	15.111	9.889	15.111
	Accurate	7.651	9.735	6.349	16.223	9.266	16.572
Stage 2	Observed	5.667	6.333	6.667	5.000	7.889	4.889
	Predicted	5.163	6.837	8.062	3.605	9.732	3.046
$\chi^2$		0.097		0.949		1.635	
<i>df</i>		1		1		1	
<i>P</i>		0.756		0.330		0.201	

Table 4.1: Observed and expected mean proportion of consumption by *F. auricularia* of *Ps. calceolariae* nymphs (*P. c.* nymphs), *E. postvittana* larvae (*E. p.* larvae) and egg masses ( $\text{mm}^2$ ) (*E. p.* eggs) over 24 hours in field cages; Stage 1 with no prey choice, or Stage 2 with prey choice available.

*P. opilio* showed no preference between the two pest species, but there was a preference between the two *E. postvittana* prey types. No preference was observed by *P. opilio* when given a choice between *Ps. calceolariae* nymphs and *E. postvittana* larvae ( $\chi^2 = 0.097$ ,  $P = 0.756$ ), or *Ps. calceolariae* nymphs and *E. postvittana* eggs ( $\chi^2 = 0.750$ ,  $P = 0.387$ ) (Table 4.2). Consumption of *E. postvittana* larvae by *P. opilio* was lower than predicted when *E. postvittana* egg masses were available ( $\chi^2 = 4.298$ ,  $P = 0.038$ ) (Table 4.2). There was 47.7% more area of egg masses eaten than predicted and 48.7% less larvae. For both predator species

there was random association with *Ps. calceolariae* relative to *E. postvittana*.

When comparing consumption of prey between predator species, similar patterns to laboratory experiments Chapter 3 were observed in the the field cages. *F. auricularia* had higher consumption rates of *Ps. calceolariae* ( $P < 0.000$ ) nymphs and *E. postvittana* larvae ( $P < 0.000$ ) than that of *P. opilio*, predating upon 51.6% and 57.3% more prey respectively (Figure 4.1). There was no clear difference in the consumption of *E. postvittana* eggs by *F. auricularia* and *P. opilio* ( $P = 0.098$ ) (Figure 4.1).

		Treatment 1		Treatment 2		Treatment 3	
		<i>P. c.</i>	<i>E. p.</i>	<i>P. c.</i>	<i>E. p.</i>	<i>E. p.</i>	<i>E. p.</i>
		nymphs	larvae	nymphs	eggs	larvae	eggs
Stage 1	Observed	3.667	5.667	3.667	4.000	5.667	4.000
	Accurate	3.471	5.802	3.037	4.778	4.149	6.106
Stage 2	Observed	2.667	5.222	4.667	3.000	5.000	5.111
	Predicted	2.953	4.936	5.537	2.130	7.436	2.675
$\chi^2$		0.059		0.750		4.298	
$df$		1		1		1	
$P$		0.809		0.387		0.038	

Table 4.2: Observed and expected mean proportion of consumption by *P. opilio* of *Ps. calceolariae* nymphs (*P. c.* nymphs), *E. postvittana* larvae (*E. p.* larvae) and egg masses ( $\text{mm}^2$ ) (*E. p.* eggs) over 24 hours in field cages; Stage 1 with no prey choice, or Stage 2 with prey choice available.

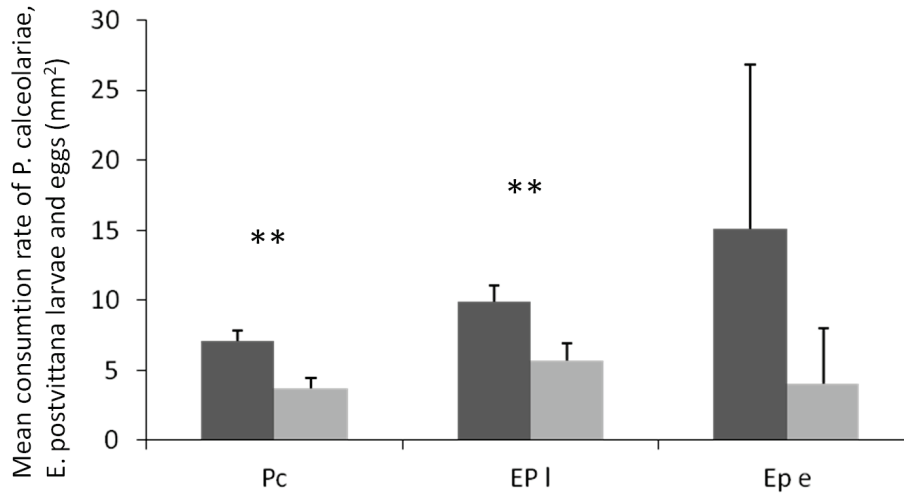


Figure 4.1: Observed mean consumption rate (95% CI) of *Ps. calceolariae* nymphs (Pc), *E. postvittana* larvae (Ep l) and egg masses (Ep e) ( $\text{mm}^2$ ) by *F. auricularia* (dark) and *P. opilio* (light) over 24 hours in field arenas (\*  $\geq 0.05$ , \*\*  $\geq 0.01$ ).

## 4.4 Discussion

Prey selection and preference has particular relevance in evaluating generalist predators as potential biological control agents. The experiments in this chapter were used to examine if predator species that had been identified in the laboratory as predators of the vineyard pests, *E. postvittana* and *Ps. calceolariae*, displayed frequency-related prey selection or if a stronger underlying prey preference influence of the consumption rates of the pest in a field-like setting. *F. auricularia* and *P. opilio* were the only species that were observed consuming *E. postvittana* from bait cards in vineyards and also consumed *Ps. calceolariae* in the laboratory experiments. Consumption in these trials bore more relevance to a open natural system because habitat complexity was incorporated into the design and *Ps. calceolariae* consumption was compared with a known prey species *E. postvittana*.

The sole significant observation of prey preference among predator and prey type combinations was the preference of *E. postvittana* eggs by *P. opilio* when given an option of *E. postvittana* larvae. However, *P. opilio* showed no preference when either *E. postvittana* prey type was combined with *Ps. calceolariae* nymphs. While a prey preference can limit suitability for managing multiple pests, in this situation it does not limit the potential of *P. opilio* to be used as a potential biological control agent of both pest species, or solely *E. postvittana* as *P. opilio* was observed consuming both prey types in vineyards (Chapter 2) (Merfield et al., 2004). A preference for eggs may be beneficial for combining *P. opilio* with the parasitoid *D. tasmanica* for vineyard management of *E. postvittana*, as predation by *P. opilio* may have a decreased impact on the population recruitment of *D. tasmanica* (Hogg et al., 2013; Paull et al., 2012)

Taplin (2007) developed on the method of Underwood and Clarke (2005) and addressed limitations raised by Manly (2006) and Underwood and Clarke (2006), to develop this predator-prey preference analysis further. The main component that was introduced was detailing the order in which prey are consumed, to encompass the shifting electivity as one prey type becomes depleted before the other. Recording the order in which the prey types are consumed and giving a greater weighting to prey eaten earlier incorporates changes in density or dispersion affect the electivity of the interaction between predator and prey. The analysis could also account for shifts in acceptability if the preferred prey type has a behavioural or physiological response to the predator pressure. In this experiment, it was not possible to observe all arenas continuously to record the order of prey type predation. To minimise the shift in electivity, an excessive amount of prey was used in the arenas.



In the laboratory consumption rate trials of Chapter 3, *F. auricularia* consumed more of each prey type than *P. opilio* and this was consistent for *Ps. calceolariae* nymphs and *E. postvittana* larvae in this chapter. It could be speculated that *F. auricularia* would be a more effective biological control agent because of the higher consumption rate per individual. That could be tempered by other criteria such as; habitat carrying capacity and manageability of the predator species, interactions interfering with pest predation, undesired effects on other beneficial or native species, and intra-guild predation (Symondson et al., 2002; Louda et al., 2003; Vance-Chalcraft et al., 2007).

The design of this experiment simplified the vineyard ecosystem to isolate prey preference, limiting effects of intra- and inter-specific interactions of predators. To gain a more complete understanding of the predator-prey interactions, more factors would need to be included to develop a practicable management tool. Wider prey choice, intra-guild interactions, giving-up densities, and foraging history may alter foraging behaviour (Louda et al., 2003; Murdoch, 1969; Brown, 1988; Symondson et al., 2002; Charnov, 1976; Riechert and Lockley, 1984). For example, the invasive Argentine ant (*Linepithema humile* (Hymenoptera: Formicidae)) has been observed to disrupt predation by tending mealybug species for their honeydew (Daane et al., 2007). While this has not been observed in New Zealand (Charles et al., 2010), other ant species have been observed tending *Ps. calceolariae* in New Zealand (Charles, 1993).

No negative or positive preference for *Ps. calceolariae* relative to *E. postvittana* was observed for *F. auricularia* and *P. opilio*. There is often some level of stenophagy or oligophagy in many "generalist" predators (Symondson et al., 2002); therefore, comparing *Ps. calceolariae* preference by these predators against *E.*

*postvittana* illustrates that there is potential for further investigation. A frequency-dependent prey selection without preference influences is promising for progressing investigation using generalists for managing multiple pests (Riechert, 1999; Schmitz, 2007; Hogg et al., 2013). However, alternative prey species and other intra-guild predators to these pest species were excluded from these trials which may alter the dynamics of the observed, or lack of, preferences (Cardinale et al., 2003; Symondson et al., 2002).

The experiments were limited to a temporal snapshot of the consumption rates to give an introduction to the interactions between individuals of predator species and combinations of pest species. By expanding the timespan of the experiment, varying the densities of the prey types, measurements over time, or increasing the community diversity, further insight could be gathered into the strength of the predator-prey relationships and the functional response of the predator species (Vance-Chalcraft et al., 2007; Carrillo and Peña, 2012). Investigations into these aspects of the predator species could present greater logistical issues, whether in arenas or vineyard environments, but should be addressed to develop and implement a successful management tool.

In developing a CBC protocol with generalist predators to complement existing management of *E. postvittana* with *D. tasmanica*, there is potential to provide a secondary benefit of controlling an additional pest, *Ps. calceolariae*. This possibility arises from no preference being displayed by *F. auricularia* and *P. opilio* for either pest species in the vineyard microcosms. Further work is needed to understand wider inter- and intra-specific interactions of generalist predators, whose greater range of inter-specific interactions could help provide improved sustainable pest control and stability to the vineyard ecosystem.



## Chapter 5

# Linear and non-linear effects of generalist predator interactions on vineyard pests.

### Abstract

The possibility of negative interactions with beneficial species is a major concern when employing a new species as a biological control agent. In addition to potential synergisms between natural enemies, the possibility of negative effects are heightened when considering generalist species. The interactions between three generalist invertebrate predators, *Anystis baccarum*, *Forficula auricularia* and *Phalangium opilio*, were examined for non-linear effects on predation of the vineyard pests *Epiphyas postvittana* and *Pseudococcus calceolariae*. In vine microcosms, combinations of the predator species were presented with either *Ps. calceolariae* nymphs, *E. postvittana* eggs or larvae. Pest predation was then compared against the expected additive (linear) consumption rate, and variations from this expected consumption rate was then interpreted as indicating either syner-

gistic or antagonistic interactions. The only consistent outcome across predator combinations and prey types was the additive effect of the three predator species assemblage. Interestingly, this was also reported in assemblages which included prey that *A. baccharum* were not observed attacking when segregated. *F. auricularia* consumed the most of all prey types, although when presented with *E. postvittana* eggs, antagonistic interactions were detected when paired with the either of the predator species, and again with *P. opilio* when given *Ps. calceolariae* nymphs. Pairwise combinations with *A. baccharum* and either alternative predator species resulted in higher predation of *E. postvittana* larvae than hypothesised. No instances of intra-guild predation occurred. The range of outcomes from different pairwise combinations of predators for each prey type highlights the complexity of intra-guild interactions. These results will also help inform future research and vineyard management. Mitigation of antagonistic interactions with inclusion of *A. baccharum* in assemblages is worth consideration when developing a biological control practice for managing *E. postvittana*.

## 5.1 Introduction

Predation and competition are central to the species composition of ecosystems and to the interactions between species within these systems. Specialist natural enemies have historically been desired as biological control agents, in part because, in contrast to generalist predators, there is a perceived limited risk of specialists disrupting desired prey, parasitoids and other predator species (Symondson et al., 2002; Chang and Kareiva, 1999; Chailleux et al., 2013). Given the wider range of interactions that generalist natural enemies have with other natural enemies and alternative prey species can lead to unintended impacts in agricultural systems (Chailleux et al., 2014; Ives et al., 2005). While interest and support for using assemblages of natural enemies that include generalist species to improve crop

yield and quality has increased, careful consideration of possible negative impacts is needed (Hooper et al., 2005; Chailleux et al., 2014; Long and Finke, 2014; Ives et al., 2005).

Utilising an assemblage of natural enemy species can improve on biological control by a single species, particularly with a pest species that have distinct variation in developmental stages, behavioural plasticity and diverse habitat use (Tylianakis and Romo, 2010; Schmitz, 2007). Creating a diverse assemblage of predators to manage a pest species can also improve biological control resilience if one of the predator assemblage is disturbed or inhibited during a season (Hooper et al., 2005; Schneider and Brose, 2013). If a generalist predator, or an assemblage which includes generalist predator species, are to be successfully applied as biological control, it is important to identify and address the interactions that these predators have with other beneficial species. The effects of both negative and positive interactions between higher trophic species on the control of pests are often complex and can be very difficult to determine (Long and Finke, 2014; Hogg et al., 2013; Chailleux et al., 2014).

*Anystis baccarum* (Prostigmata: Anystidae), *Forficula auricularia* (Dermaptera: Forficulidae), and *Phalangium opilio* (Arachnida: Opiliones) co-exist in vineyards and were identified as predators of *Epiphyas postvittana* (Lepidoptera: Tortricidae) (Chapter 2). There are four expected prey effects that result from the interactions of multiple predators with a common prey species: risk-enhancing, risk-reducing, intra-guild predation (IGP), and an additive effect which is the sum of predation by species in isolation (Straub et al., 2008; Soluk and Collins, 1988; Vance-Chalcraft and Soluk, 2005a). A risk-enhancing interaction increases predation by one or both predator species, above what would be expected if there

was no interaction (Losey and Denno, 1998; Paull et al., 2012). By contrast, risk-reducing interactions reduce the expected predation due to interference between predator species and non-specific anti-predator behaviour (Rosenheim et al., 1993; Losey and Denno, 1998; Hogg et al., 2013). IGP is defined as predation of a competitor for the same prey species, an interaction that often benefits the pest population which the predators share (Sih et al., 1998; Griffen and Byers, 2006). Risk-enhancing and additive outcomes generally occur when there is less overlap in habitat use or hunting mode between the different predator species (Schmitz, 2007; Hooper et al., 2005). Complementarity between predators can have risk-enhancing effects if the prey have predator specific responses to one species that make them more exposed to another predator species, or additive response if there is minimal niche overlap and no interaction between predator species (Sih et al., 1998; Long and Finke, 2014; Schmitz, 2007).

The four interactions can be categorised as either linear or non-linear outcomes. A linear outcome would occur if there was little interaction between predator species, minimal anti-predator prey response, or if the resulting outcome of any predator interactions was the same as the expected additive pest predation rate (Sih et al., 1998; Snyder and Wise, 1999; Vance-Chalcraft and Soluk, 2005a). Non-linear outcomes can be risk-enhancing (synergistic) and risk-reducing (antagonistic) interactions, where a difference occurs between the observed and expected number of prey predated on by the predator assemblage (Sih et al., 1998; Vance-Chalcraft and Soluk, 2005a). Morphology, micro-habitat use, and behavioural responses of the predator and prey species can contribute to the non-linear outcomes from inter-predator relationships (Schmitz, 2007; Vance-Chalcraft and Soluk, 2005a) (Figure 5.1).

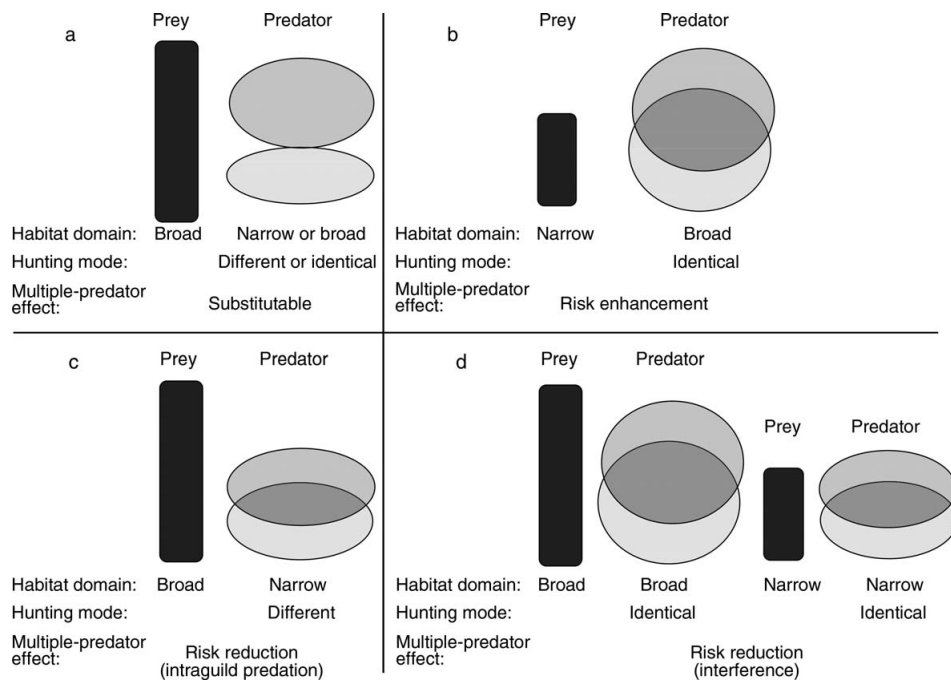


Figure 5.1: Predictions of four contingent multiple-predator effects on a common prey species derived from an empirical synthesis of multiple-predator experiments. Dark rectangles represent the prey habitat domain. Ellipses represent predator habitat domain. (a) Predators are expected to have substitutable (additive) effects whenever prey have broad habitat domains and predators have complementary (narrow or broad) habitat domains. (b) Predators are expected to have risk-enhancing effects whenever prey have a narrow domain and predators have broad, overlapping habitat domains and the same hunting modes. (c) Predators are expected to have risk-reducing effects due to intraguild predation whenever prey have a broad domain and predators have narrow, overlapping habitat domains and different hunting modes. (d) Predators are expected to have risk-reducing effects due to interference interactions when they have identical hunting modes and overlapping habitat domains with themselves and their prey (Schmitz, 2007).

When combining natural enemies, particularly generalists, there is potential for IGP to occur, an important interaction to identify when deciding their suitability for biological control. IGP is not considered a simple combination of competition and predation as it involves feedback loop on the impact on the shared prey species (Polis and Holt, 1992; Chailleux et al., 2014). In the more linear terrestrial invertebrate systems, IGP by a dominant predator is more likely to reduce risk for



prey (Vance-Chalcraft et al., 2007; Polis and Holt, 1992; Rosenheim et al., 1993). A difference in size between predator species can indicate a likelihood of IGP (Griffen and Byers, 2006; Vance-Chalcraft and Soluk, 2005b; Polis et al., 1989), such as with *A. baccarum* and the comparatively larger *F. auricularia*. While IGP does not automatically provide a release from predation pressure for the prey, it suggests a single predator may be more suitable for biological control than an assemblage (Vance-Chalcraft et al., 2007; Rosenheim et al., 1995).

There are two widely used experimental designs for examining intra-guild interactions between predator species: additive and replacement series experiments (Schmitz, 2007; Byrnes and Stachowicz, 2009). In an additive design, the sum of the mean consumption rate by individuals of each predator species is used to estimate the linear consumption rate when individuals of both predator species are combined, deviation from the estimated consumption indicates a non-linear predator relationship (Schmitz, 2007; Sih et al., 1998). An additive experimental design is more suitable for isolating any non-linear interactions between predator species which utilise a common prey because only a single predator of each species is used, removing any intra-specific influences (Schmitz, 2007; Northfield et al., 2014; Sih et al., 1998).

Replacement series experiments are similar to additive except multiple predators of each species are used and predator density remains consistent, regardless if either a single predator species or an assemblage of predator species are used (Schmitz, 2007; Sih et al., 1998). A replacement series design incorporates both intra- and inter-specific interactions, as non-linear interactions can occur within a species. While this design removes any effect of increasing predator density, as in the additive design, attributing non-linear outcomes is confounded by hav-

ing interactions between and within predator species (Schmitz, 2007; Northfield et al., 2014). Where possible, it is desirable to run both experimental designs concurrently (Griffen and Byers, 2006; Schmitz, 2007; Byrnes and Stachowicz, 2009; Griffen, 2006).

The outcomes of inter-specific interactions between predators *A. baccarum*, *F. auricularia*, and *P. opilio* were examined with either *E. postvittana* or *Pseudococcus calceolariae* (Hemiptera: Pseudococcidae) as prey in additive experiments to isolate the intra-specific predator relationships. This design allows for the detection of pair-wise interactions, and also presents outcomes of the three predator assemblage with either pest species. Examining how these generalist predator species interact helps to inform further research into developing a protocol that incorporates them to manage vineyard pests.

## 5.2 Methods

*The arenas, field site, and collection of invertebrates were unchanged from Chapter 4.*

### 5.2.1 Field site

Cossars Vineyard was used for prey preference trials, situated south of Christchurch, New Zealand, between the Halswell River and the Port Hills, near Tai Tapu, 9.5 km from Lincoln University. In the 2011-2012 summer growing season, vineyard management was limited to maintaining appearance for a neighbouring hospitality venture. The only cultivar used was Chardonnay, and all vine rows used in this experiment were in one vineyard block.

### Experimental cages

BugDorm<sup>™</sup> tube shaped cages (MegaView Science Co., Ltd., Taichung, Taiwan) were 700 mm long x 300 mm diameter (41 x 37 mesh/10 mm<sup>2</sup>) with each end cinched tight around the cane by a draw cord. In the centre of the cage there was a clear plastic band for viewing and a zip ran the length of the cage so that the tube could be opened to lie flat. To ensure no insect could enter or leave, a plastic cable tie was pulled tight over the ends of the cage next to the draw cord.

The leaves on canes were trimmed so that six remained with a total spread of less than 500 mm to standardise the arena complexity and area, and so cages could fit over canes comfortably. These cages restricted predator and prey dispersal while still containing aspects of the vine canopy habitat complexity. Pyrethrum (Yates<sup>®</sup>, Nature's Way Pyrethrum) was sprayed thoroughly on to each cane prior

to the cage being secured to ensure other invertebrates were removed. Arenas were left for at least 48 hours before experiments commenced, to exceed the 24 hour withholding period of the pyrethrum treatment so invertebrates involved in experiments were unaffected.

### 5.2.2 Arthropods used

#### Predator species

*F. auricularia* and *P. opilio* were collected as described in Chapter 3, from the organic Biological Husbandry Unit (BHU) ([www.bhu.org.nz](http://www.bhu.org.nz)), Lincoln University. Sex of predators were not considered as no significant difference was observed between sexes in consumption rates in laboratory experiments (Chapter 3). One individual predator was used per arena so consumption rates would not be influenced by intra-specific and inter-predator interactions.

*F. auricularia* was collected from a peach orchard (*Prunus persica* var. *persica*) at the BHU. Strips of corrugated cardboard, approximately 200 mm wide, were wrapped around the branches of the trees with the corrugated side against the bark and stapled to hold the resulting tube in place. These shelters were opened above a collection tray and adults were identified by the presence of hind wings extending past the tegmina. *P. opilio* was collected by hand from riparian strips and areas of long rank grasses around the BHU; only adult specimens (body length  $\geq 5$  mms) were used. *A. baccarum* were caught in the Lincoln University vineyard by beating the vine canopy and capturing large specimens that fell on to the beating tray. Of every group of 30 large individuals caught, the largest ten (judged by eye) were used in trials.

## Prey species

Three different prey types were used; *E. postvittana* larvae (7.5 - 8.5 mm long), *E. postvittana* egg masses, and *Ps. calceolariae* nymphs (2 - 2.5 mm). Prey were supplied by New Zealand Institute for Plant & Food Research Ltd, Auckland. The prey types used in the experiment were those predated on by more than one of the predator species in Chapter 3. For each prey type, there were seven different treatments with differing predator combinations in the cages; three treatments of a single predator species (Stage 1), three treatments of each two-way combination of predator species (Stage 2), and one treatment of all three predator species (Stage 2). Control cages without predators were run with each prey type to gauge the background mortality of prey types.

The number of prey individuals assigned to each predator were in excess of the maximum consumption rates for each prey type found in preliminary trials. For all trials of each prey type, the sum of the excess prey quantities for the three predator species was placed into arenas; 22 *E. postvittana* larvae, 145 mm<sup>2</sup> of *E. postvittana* egg masses, and 13 *Ps. calceolariae* nymphs. This ensured the initial prey density and chance of encounter was equivalent across treatments for each prey type.

*E. postvittana* egg masses arrived laid on sheets of waxed paper which were cut into smaller pieces. The area of each piece was measured to the nearest mm<sup>2</sup> and the target area for treatments was made up from four pieces of paper with egg masses. Four of the six leaves within a cage had egg masses attached. These were stapled to the abaxial surface of separate leaves in the arena. Egg masses with existing damage were excluded from trials to ensure predators were not attracted by cues from damaged eggs and that any damage could be clearly attributed to

predators. *E. postvittana* egg masses are clumped and not able to disperse, unlike the other prey types, so egg masses were dispersed in cages across the leaves as widely as practicable to mitigate this issue. The eggs were not placed on the upper side of leaves to minimise dessication (Danthanarayana, 1983).

### 5.2.3 Experimental protocol

Trials comparing the effect of intra-guild interactions between *F. auricularia*, *P. opilio* and *A. baccarum* on predation of *E. postvittana* and *Ps. calceolariae* were run concurrently from February 2012 to April 2012. After capture, predators were starved in individual Petri dishes with damp dental rolls for 48 hours in a controlled environment (18 °C ( $\pm 2$  °C), 16 h light: 8 h dark). Prey items were measured and sorted in the laboratory prior to leaving for the vineyard. The appropriate prey types were released into randomly assigned cages, then were left to acclimatise and disperse throughout the arena for 24 hours before predators were introduced.

The trials ran for 24 hours from the time predators were introduced into the cages. After this period, the cages remained closed but the cane was cut from the vine and taken back to the laboratory. Arenas were opened separately and laid out flat so no specimens could hide in folds of the cage, and care was taken to ensure nothing escaped. Predators were collected first as they were more mobile and placed individually into labelled vials of high grade ethanol. Each leaf was removed and searched thoroughly for prey items then discarded, followed by the vine cane. The number of live *E. postvittana* larvae and *Ps. calceolariae* nymphs remaining, as well as the area of remaining undamaged *E. postvittana* egg masses

in each arena were all recorded.

#### 5.2.4 Analysis

Hypothesised consumption rates for predator interactions were calculated by combining the mean proportion of prey consumed by predators species A ( $p_a$ ) and species B ( $p_b$ ) from Stage 1 (no inter-specific interactions) into a multiplicative model (Sih et al., 1998; Soluk and Collins, 1988; Schmitz and Sokol-Hessner, 2002). For each prey type, the proportion consumed by different combinations of predator species (Stage 2) ( $P_{ab}$ ) were compared against a hypothesised consumption rate with a two-tailed one sample t-test. The null hypotheses of no intra-guild interaction where the hypothesised consumption rate, derived from predation in Stage 1 and the multiplicative model, did not significantly differ from the observed Stage 2 consumption rate:

$$H_0: p_a + p_b - p_a p_b = P_{ab},$$

$$\text{or: } p_a + p_b + p_c - p_a p_b p_c = P_{abc}$$

Consumption rates for all single predator treatments of each prey type were tested with a one-way ANOVA. Prey types with significant differences were further examined with two-sample t-tests to identify which predator species varied in consumption rates.

### 5.3 Results

Larvae predation in both pairwise predator treatments with *A. baccharum* and either *P. opilio* ( $\bar{x} = 0.40$ ) or *F. auricularia* ( $\bar{x} = 0.56$ ) had significantly higher consumption rates than the hypothesised proportions ( $\bar{x} = 0.35$   $t = 3.03$ ,  $d.f. = 4$ ,  $p = 0.039$ ; and  $\bar{x} = 0.47$ ,  $t = 4.96$ ,  $d.f. = 4$ ,  $p = 0.008$ , respectively). There was no significant difference in the proportion of larvae predated on in the treatment of *P. opilio* and *F. auricularia* from the estimated ( $t = -0.42$ ,  $d.f. = 4$ ,  $p = 0.690$ ), or with all three predator species ( $t = -1.58$ ,  $d.f. = 4$ ,  $p = 0.190$ ). Predation of larvae by single predator species varied significantly ( $p = 0.000$ ,  $F = 72.11$ ), *F. auricularia* was the highest predator of larvae and *A. baccharum* the lowest (Figure 5.5, A).

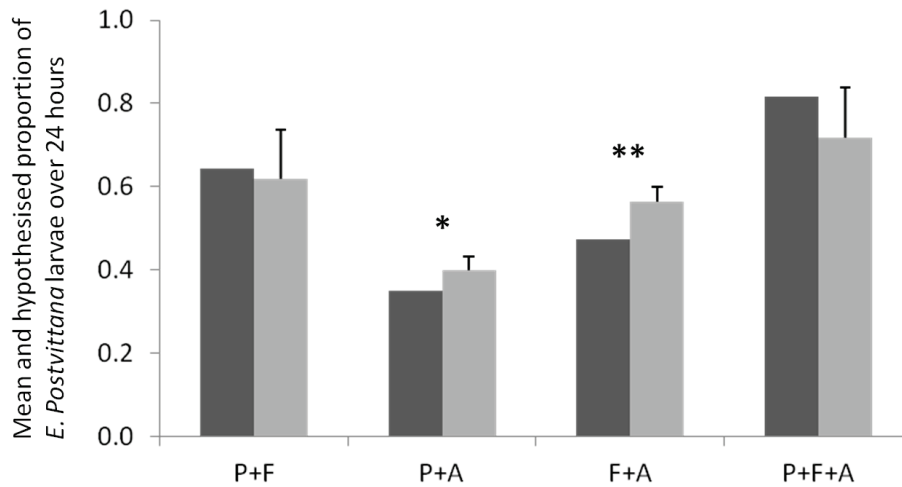


Figure 5.2: Hypothesised (dark) and observed (light) (95% CI) mean proportion of *E. postvittana* larvae consumed over 24 hours in vineyard field cages by; *P. opilio* and *F. auricularia* (P+F), *P. opilio* and *A. baccharum* (P+A), *F. auricularia* and *A. baccharum* (F+A), and *P. opilio*, *F. auricularia* and *A. baccharum* (P+F+A) (\*  $\geq 0.05$ , \*\*  $\geq 0.01$ ).

The proportion of *E. postvittana* egg masses predated on by *F. auricularia* in



combination with either *P. opilio* ( $\bar{x} = 0.09$ ) or *A. baccharum* ( $\bar{x} = 0.05$ ) were both significantly lower than the hypothesised consumption rates ( $\bar{x} = 0.20$ ,  $t = -3.42$ ,  $d.f. = 6$ ,  $p = 0.014$ , and  $\bar{x} = 0.20$ ,  $t = -6.03$ ,  $d.f. = 6$ ,  $p = 0.001$  respectively) (Figure 5.3). There was no significant interaction between *P. opilio* and *A. baccharum* or three predator species treatment that affected *E. postvittana* egg predation. *F. auricularia* had the highest consumption rate ( $p = 0.001$ ,  $F = 11.27$ ), but no significant difference was observed between *P. opilio* and *A. baccharum* consumption rates (Figure 5.5, B).

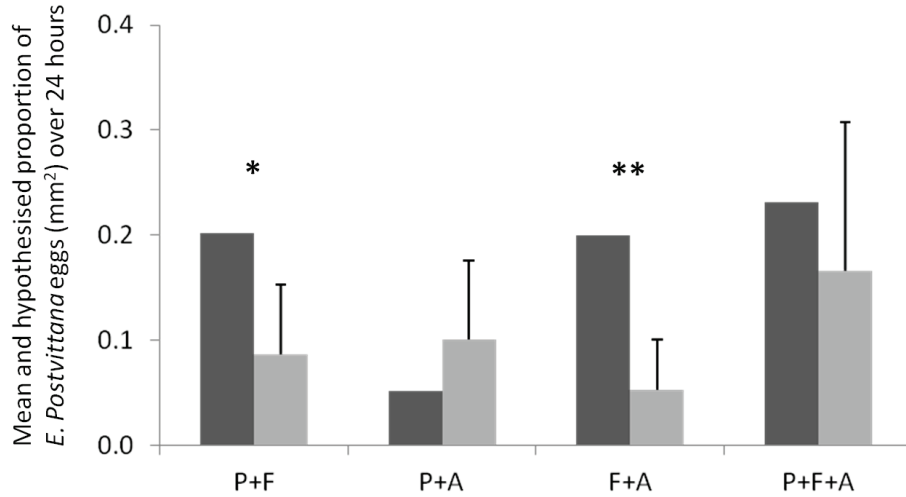


Figure 5.3: Hypothesised (dark) and observed (light) (95% CI) mean proportion of *E. postvittana* egg mass area (mm<sup>2</sup>) consumed over 24 hours in vineyard field cages by; *P. opilio* and *F. auricularia* (P+F), *P. opilio* and *A. baccharum* (P+A), *F. auricularia* and *A. baccharum* (F+A), and *P. opilio*, *F. auricularia* and *A. baccharum* (P+F+A) (\*  $\geq 0.05$ , \*\*  $\geq 0.01$ ).

The only interaction between predator species that significantly influenced *Ps. calceolariae* nymph consumption rates was the *F. auricularia* and *P. opilio* treatment ( $\bar{x} = 0.40$ ) being significantly lower than the hypothesised consumption rate ( $\bar{x} = 0.55$ ,  $t = -4.16$ ,  $d.f. = 5$ ,  $p = 0.009$ ) (Figure 5.4). In all treatments that included *A. baccharum* there was no observed affect from any predator interaction

on *Ps. calceolariae* predation. Comparisons of consumption rates of nymphs in single predator treatments ( $p = 0.000$ ,  $F = 45.82$ ), found *P. opilio* and *F. auricularia* were similar but none were predated on by *A. baccharum* (Figure 5.5, C).

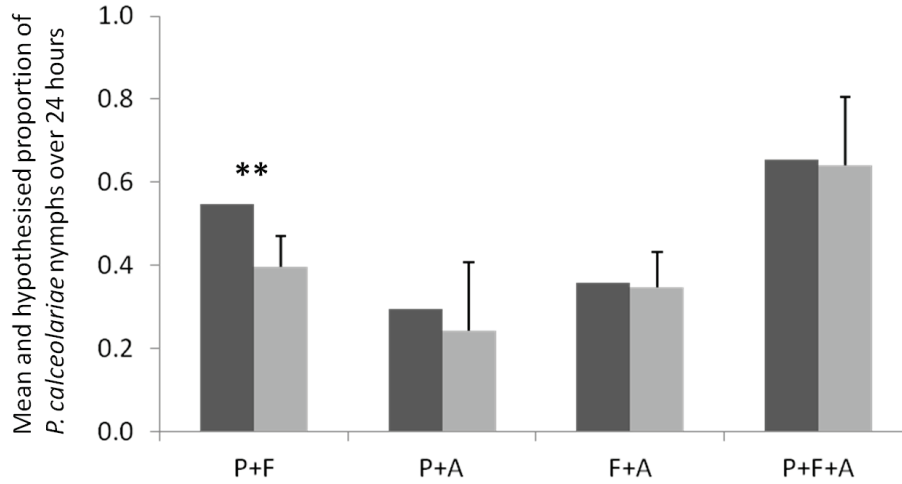


Figure 5.4: Hypothesised (dark) and observed (light) (95% CI) mean proportion of adult female *Ps. calceolariae* consumed over 24 hours in vineyard field cages by; *P. opilio* and *F. auricularia* (P+F), *P. opilio* and *A. baccharum* (P+A), *F. auricularia* and *A. baccharum* (F+A), and *P. opilio*, *F. auricularia* and *A. baccharum* (P+F+A) (\*  $\geq 0.05$ , \*\*  $\geq 0.01$ ).

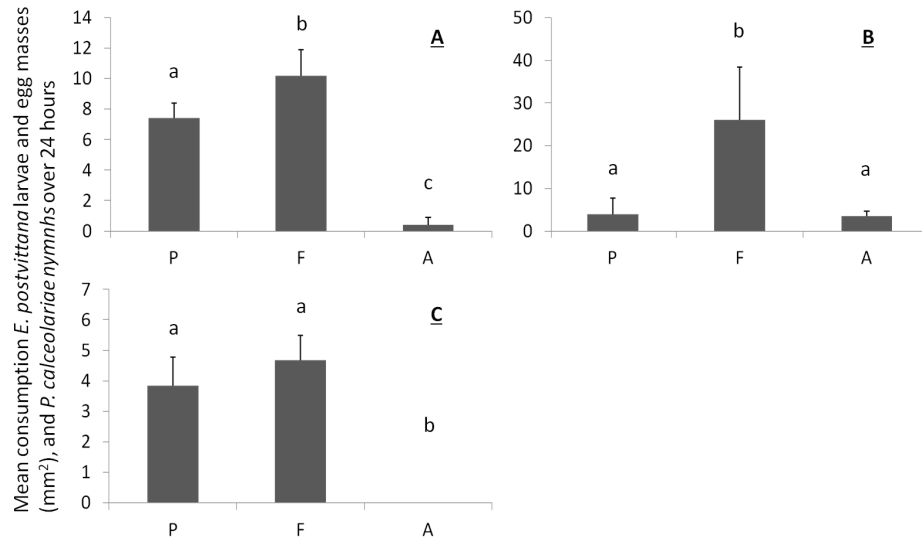


Figure 5.5: Mean consumption rates in vineyard field cages over a 24 hour period (95% CI) of *E. postvittana* larvae (A) and eggs (mm<sup>2</sup>) (B), and *Ps. calceolariae* nymphs (C) by *P. opilio* (P), *F. auricularia* (F) and *A. baccharum* (A).

## 5.4 Discussion

By using these simplified assemblages of predator and prey species, it was possible to identify the nature of the interactions between these predators of *E. postvittana* in vineyards cages. A range of synergistic, neutral and antagonistic interactions were observed amongst the various combinations of predator and prey types. Predator interactions are complex and difficult to predict, but by these basal relationships can be used to indicate how promoting one species or the other might affect the pest population in the presence of intra-guild predator species (Schneider and Brose, 2013; Chailleux et al., 2014).

Across the three prey types presented, the only consistent outcome of additive predator interactions occurred when all three predator species, *P. opilio*, *F. auricularia* and *A. baccharum* were combined. *E. postvittana* larvae were the only prey with which *P. opilio* and *F. auricularia* did not interact antagonistically, but

rather an additive outcome was observed. The combination of *P. opilio* and *A. baccharum* enhanced *E. postvittana* larvae predation risk but this was not consistent with *E. postvittana* eggs and *Ps. calceolariae* nymphs where additive outcomes occurred. *F. auricularia* and *A. baccharum* interactions had varied impacts on pest predation; enhanced *E. postvittana* larvae predation risk, reduced *E. postvittana* egg predation risk, and an additive outcome with no significant difference in *Ps. calceolariae* predation from the hypothesised consumption rate. *A. baccharum* predation of *E. postvittana* larvae without another predator species present was an unexpected result. Although minimal amounts of *E. postvittana* were predated on in laboratory trials, *A. baccharum* was not observed predating on medium sized larvae, only first instar larvae (Chapter 3).

The assemblage of all three predator species identified as the predominant predators of *E. postvittana* in vineyards (Chapter 2) negated any non-linear predator relationships of prey predation that occurred in any pair-wise predator treatments. Without knowing the underlying mechanisms of the interactions, it is unclear whether no interactions occurred, or whether some form of compensation cancelled out any non-linear interactions (Paull et al., 2012; Sokol-Hessner and Schmitz, 2002; Hogg et al., 2013). Some form of behavioural change or compensatory effect by either the prey or predator species occurred because for each prey type there was a non-linear interaction in at least one of the pairwise treatments (Sih et al., 1998). The complementary result would indicate that there should be greater reduction of the pest species by multiple predator species than by any single species.

Predation of *E. postvittana* larvae increased in both pair-wise treatments with *A. baccharum*, though this effect was not apparent in the three-way predator species

treatment. Disturbance from silk covered leaf roll refuges has been shown to make first instar *E. postvittana* larvae more vulnerable to *A. baccharum* predation (Paull et al., 2012). *F. auricularia* have been observed feeding on larvae within silk leaf rolls (Danthanarayana, 1983), but *A. baccharum* could not access larvae in refuges (Paull et al., 2012). The higher consumption rate of *P. opilio* than *A. baccharum* may indicate they are able access larvae in leaf rolls. The observed increase in larvae predation may be due to larger predators inducing a behavioural response in the *E. postvittana* larvae, making them prone to increased predation by *A. baccharum* outside their silk leaf rolls.

The antagonistic interactions between *P. opilio* and *F. auricularia* with *Ps. calceolariae* nymphs did not occur when *A. baccharum* was present. There was no divergence from the null hypothesis for any pairwise treatment in any treatment involving *A. baccharum*. This does not necessarily mean that *A. baccharum* attacked any nymphs in the three-way treatment, no evidence of predation on *Ps. calceolariae* nymphs was observed in this work and in laboratory conditions (Chapter 3). There was likely an indirect mediating mechanism that negated the antagonistic pairwise interaction of *P. opilio* and *F. auricularia* (Sih et al., 1998; Chailleux et al., 2014).

The additive outcome on the predation of *E. postvittana* egg masses by the combination of *P. opilio* and *A. baccharum* was contrary to the synergistic relationship expected as discussed in previous chapters. In Merfield et al. (2004), predatory mites (*Balaustium* species (Acari: Erythraeidae)) and manually pierced eggs increased predation of brown blowfly, (*Calliphora stygia* (Diptera: Calliphoridae)), by *P. opilio*. The facilitative predatory mite species and invertebrate egg prey species were different in these experiments so the possible cues given off by

the damaged blowfly eggs or extent of damage by *Balaustium* species may have been differed to induce increased predation by *P. opilio*. Alternatively, the artificially high prey density and extended time period may make shifts in predation due to predator interactions less apparent (Vance-Chalcraft et al., 2007).

All antagonistic interactions that were observed involved *F. auricularia*, whereas only one of the synergistic interactions occurred with *F. auricularia*, and *A. baccharum*, enhancing predation risk for *E. postvittana* larvae. Predation risk was reduced in both pair-wise treatments for *E. postvittana* eggs that included *F. auricularia*, and with *P. opilio* for *Ps. calceolariae*. *F. auricularia* may behave as a dominant predator due to it's larger size and interfering with smaller competitors, and intra-guild predation may become apparent at lower prey densities (Griffen and Byers, 2006; Vance-Chalcraft and Soluk, 2005b; Vance-Chalcraft et al., 2007).

The linear interactions with the three predator assemblages indicate predator complementarity occurred, or that any non-linear relationships that did occur were negated (Schmitz, 2007; Vance-Chalcraft and Soluk, 2005a). When predator assemblages include more species there can be averaging of predation creating an additive outcome which is what may have occurred with the experimental assemblages (Schmitz and Sokol-Hessner, 2002; Schmitz, 2009). While linear interactions were observed in these trials, there was an excess of prey available and it would be prudent to test these relationships at lower densities of prey and in replacement-series experiments. At lower prey densities, the nature of the interactions may alter when predators are less inundated with prey and can alter the linearity of the predator species interactions (Vance-Chalcraft and Soluk, 2005b; Soluk, 1993; Schmitz, 2009). Densities within field cages can be abnormal and constraints of the cages may limit normal foraging behaviour (Symondson et al.,

2002; Vance-Chalcraft et al., 2007).

In the models produced by Schmitz (2007) (Figure 5.1), hunting mode and the habitat range of prey and predators influence the predicted effect on prey predation due to the predator species interaction. The range and variety of linear and non-linear relationships for predator species and prey types observed could indicate that habitat use or hunting mode may shift relative to the prey items presented. If there was behavioural plasticity, then there is potentially greater scope for divergence between predators when a greater range of habitat and prey are present in an open vineyard system (Schmitz, 2007; Chang and Kareiva, 1999; Ives et al., 2005). A decrease of overlap in habitat use and hunting mode can benefit synergistic and additive predator effects (Schmitz, 2007) (Figure 5.1).

Intra-specific predator interactions, such as territoriality or cooperation, were excluded in these experiments which could occur in vineyard ecosystems. Cannibalism is an important interaction which can occur with each of the three predator species (Cuthbertson and Murchie, 2004; Solomon et al., 2000; Bristowe, 1949). Compared to IGP, cannibalism has been shown to have lessened numeric impact on populations of generalist predatory mites due to higher nutritional reward (Schausberger and Croft, 2000; Schausberger and Walzer, 2001; Polis et al., 1989). Inclusion of con-specific predators and a wider range of micro-habitats in a replacement series experiment are necessary to develop investigations of biological control by generalists as context is important in inter-specific interactions (Byrnes and Stachowicz, 2009; Tylianakis and Romo, 2010). The additive design has given a snapshot of interactions between generalist predator species to indicate how these species interact directly. A replacement series experiment would add intra-specific influences and draw attention to how these interactions are altered

(Schmitz, 2007).

No one predator species clearly stood out as a leading candidate for use as a biological control agent, but the results of this work will help to predict and understand the interactions in further research. Understanding the mode of hunting the pests and movement in the vineyard environment in finer detail would aid in predicting the effectiveness of these predators as management tools of *E. postvittana* and *Ps. calceolariae* (Schmitz, 2007; Straub et al., 2008; Wilby et al., 2005). Habitat use by predators may shift throughout a growing season as a prey species develop over a season or relative prey species densities alter, which may affect predator species interactions. The variation of outcomes for each species in these simplified systems highlights the complexity intra-guild interactions between predators. However, the effects of the interactions could be used to direct future research and to the benefit biological control.



## Chapter 6

# Discussion

### 6.1 Introduction

A shift towards utilising conservation biological control (CBC) as part of a strategy to improve the sustainability of primary production is increasing (Cullen et al., 2008; Jonsson et al., 2008; Cuthbertson et al., 2014). Through this change, there is growing opportunity to use generalist predator species as biological control agents, which however are often perceived to be unsuitable for pest management (Symondson et al., 2002; Chang and Kareiva, 1999). Historically, specialised natural enemies have been used in classical or augmentative biological control to minimise impacts on beneficial and non-pest species (Chang and Kareiva, 1999). The reluctance and concerns often associated with generalist species are reduced with CBC because species that already exist in the environment are used. However, the potential risks of using generalists and the impacts for other beneficial and desired species are not entirely removed. The range and nature of interactions still need to be considered when evaluating the viability of using generalist natural enemies in pest management (Losey and Denno, 1998). Development of CBC practices still need thorough investigation to confirm the effectiveness and

suitability of a new method of pest control in order to be adopted into management (Cullen et al., 2008; Naeem et al., 2015).

Enhancing ecosystem services such as biological control within agricultural systems or those from the surrounding environments has been an inherent part of agriculture since its inception; but the concept has recently been articulated and gained in popularity as an alternative to classical or augmentative biological (Landis et al., 2000; Jonsson et al., 2008; Tscharntke et al., 2012). Classical biological control involves introducing and establishing a natural enemy into an environment to control a pest, often an enemy that has co-evolved with the pest elsewhere (Eilenberg et al., 2001). This form of control can be highly effective, requiring little ongoing management when successful; however, prior to release, extensive investment and research is needed as success rates are often low and negative impacts can be costly (Greathead and Greathead, 1992; Gurr and Wratten, 1999). Augmentative biological control needs infrastructure to maintain populations of predators or parasitoids for periodic inundative or early-season inoculative releases that may not persist in the target environment (Collier and van Steenwyk, 2004; Bale et al., 2008).

An advantage of managing pest species with CBC is the availability of generalist predator species, as the risk of displacing or affecting non-target species is minimised, relative to other forms of biological control. A lack of some degree of oligophagy has traditionally been seen as a negative of generalist species as their populations are thought to be independent of change in a pest population, which could divert their predation effort from the target pest and negatively impact beneficial species (Symondson et al., 2002; Chang and Kareiva, 1999). While these concerns are not unfounded, rigorous investigation prior to implementing

generalist predators can determine suitable species, as examples and theory have shown their potential to be successful in biological control (Cuthbertson et al., 2014; Hogg et al., 2014; Long and Finke, 2014; Symondson et al., 2002). Often generalist predators are less responsive to pest population increase but are often able to persist throughout the year, partly by consuming non-pest prey, and in turn provide an early season or a “lying-in-wait” strategy for pest management and inhibiting pest recruitment (Chailleux et al., 2014; Chang and Kareiva, 1999; Settle et al., 1996).

The investigation of possible generalist predator species to be included as part of vineyard pest management in the preceding chapters focussed on two pests of vines, *Epiphyas postvittana* (Lepidoptera: Tortricidae) and *Pseudococcus calceolariae* (Hemiptera: Pseudococcidae). *E. postvittana* is a native of Australia that has successfully invaded a range of locations globally and is a pest of a variety of pome fruit, stone fruit, citrus and is a significant pest in New Zealand’s vineyards (Suckling and Brockerhoff, 2010; Lo and Murrell, 2000; Tooman et al., 2011). The main cause of concern generated by *Ps. calceolariae* in New Zealand vineyards is vectoring the Grapevine Leafroll-associated Virus 3 which inhibits vine productivity and requires plant removal to prevent the spread of the virus (Petersen and Charles, 1997; Daane et al., 2011; Petersen and Jordan, 1992). These pest species account for a majority of the insecticide use in vineyards that adhere to Sustainable Winegrowing New Zealand®; 94% of New Zealand’s wine producing area is certified sustainable or organic (Manktelow et al., 2005; New Zealand Winegrowers, 2014).

Combining natural enemies to form an assemblage of biological control agents can enhance pest control. A diversity of hunting or searching modes and habitat

range can create a synergistic or additive outcome for pest removal when niche overlap of predators and parasitoids is minimal (Schmitz, 2007; Sih et al., 1998; Losey and Denno, 1998). However, negative impacts on ecosystem services, such as pest management, can also be created without thoroughly considering how biological agents of a potential assemblage interact, as complexities may confound expected outcomes or short-term interactions may not persist (Chailleux et al., 2014; Paull et al., 2012; Schmitz, 2007).

There is potential and precedent for creating an assemblage to manage *E. postvittana*. An existing CBC protocol for *E. postvittana* in vineyards employs supplementary planting of buckwheat (*Fagopyrum esculentum*), purple tansy (*Phacelia tanacetifolia*) and alyssum (*Lobularia maritima*) to benefit pest control by the parasitoid *Dolichogenidea tasmanica* (Hymenoptera: Braconidae) (Berndt et al., 2002; Berndt and Wratten, 2005; Berndt et al., 2006; Irvin et al., 2006; Scarratt et al., 2008). A range of positive and negative outcomes have been observed when specialist parasitoids have been combined with generalist predators in relation to pest management (Snyder and Ives, 2003; Colfer and Rosenheim, 2001; Chailleux et al., 2013; Paull et al., 2012; Hogg et al., 2013).

An example that focussed on *E. postvittana* found that an immediate synergism between *D. tasmanica* and the predatory mite, *Anystis bacarrum* (Prostigmata: Anystidae), increased predation, but modelling predicted that this would lead to decreased pest control in the long-term (Paull et al., 2012). Increased predation by mites was made possible by the act of parasitism, and predation of parasitised *E. postvittana* reduced *D. tasmanica* population recruitment (Paull et al., 2012). However, the opposite was found in California. Long-term pest control of *E. postvittana* increased with the combination of spiders and parasitoids

despite predation of parasitised larvae by spiders (Hogg et al., 2013). Predation in this instance was not reliant on the act of parasitism and recruitment of the parasitoid population was not limited due to the high fecundity of the parasitoid species (Hogg et al., 2013).

In the preceding chapters, work was done to: 1) identify the generalist predator species that were present within vineyards and which consume *E. postvittana*; 2) determine which of the predator species identified as predators of *E. postvittana* were capable of and suitable for contributing to the control a secondary pest, *Ps. calceolariae*; 3) examine the nature of the interactions between the predator species in relation to pest mortality to indicate potential outcomes of promoting one or more generalist predator species. The results can be used to help address pest management problems and to determine future research for developing generalist predators as biological agents complementary to other approaches in New Zealand and elsewhere.

## 6.2 Summary

### 6.2.1 Generalist predators of *E. postvittana*

In order to begin developing a CBC method with a generalist predator to complement *D. tasmanica*, it was necessary to identify which of the the generalist predators that occurred within the vineyard predated upon the primary pest, *E. postvittana*. A variety of generalist predator species which attack *E. postvittana* have been observed in New Zealand and elsewhere, including; *A. baccarum*, spiders, *Forficula auricularia* (Dermaptera: Forficulidae), and a variety of other taxa including opilionid, coccinellid and formicid species (Paull et al., 2012; Frank et al., 2007; Danthanarayana, 1983; Hogg et al., 2014). However, those predator species relevant to the current study system needed to be identified.

In Chapter 2, fieldwork was carried out in vineyards at Wither Hills Ltd. in Marlborough, the largest wine producing region in New Zealand, in the growing seasons of 2010/11 and 2011/12. Predator diversity surveys of the vineyard canopy and ground were carried out to give a background of the native predator potential. Comparisons relating to predator diversity and *E. postvittana* predation were made between conventional vineyards and those organically managed as part of conversion to certified organic status (BioGro<sup>TM</sup> New Zealand Ltd). Bait cards with either *E. postvittana* larvae or egg masses were placed throughout vineyards and predators present on cards were collected throughout 24 h periods in a manner similar to that of Pfannenstiel and Yeargan (2002). Finally, sentinel *E. postvittana* bait cards of larvae and eggs were used to gauge comparative removal rates between organic and conventional vineyards.

The experiments in Chapter 2 showed that the functional predator diversity

within vineyards was higher in those managed organically, and no variation of diversity was explained by season or grape variety. Predatory mites were the most abundant of the predator groups, accounting for 57% of predators collected, followed by *Phalangium opilio* (Arachnida: Opiliones), ground-running spiders, coccenellids and *F. auricularia*. Only three predator species were observed feeding on *E. postvittana* larvae and eggs; *A. baccharum*, *F. auricularia* and *P. opilio*. These predation observations were more frequent in organically managed vineyards and predation by *A. baccharum* the most widespread, feeding at 58% of egg bait cards and 46% larval bait cards across the vineyards. Despite organically managed vineyards having higher predator diversity and observations of predation of *E. postvittana* from bait cards, this did not translate to any significant difference in pest removal rates. No relationships between removal rates and season, variety and vineyard management were detected. The removal rates of *E. postvittana* eggs and larvae could not be attributed to individual predator species, as no direct observations of predation were made during this experiment.

Similar observations of *E. postvittana* consumption rates were observed in laboratory trials of maximum consumption rates and in vine canopy field cages (Chapter 3; Chapter 5). *F. auricularia* had significantly higher rates for both larvae and eggs than *A. baccharum* and *P. opilio* (Chapter 3; Chapter 5). Maximum consumption rates of *E. postvittana* egg masses by *A. baccharum* and *P. opilio* were not significantly different in laboratory or field cage experiments (Chapter 3; Chapter 5). *A. baccharum* did not consume any medium sized larvae in the laboratory despite being the most frequently observed predator attacking larvae of the same size on bait cards in vineyards (Chapter 2; Chapter 3).

Prey preference of *P. opilio* and *F. auricularia* between *E. postvittana* larvae

and eggs were examined in vineyard field cages, as preference may have connotations for implementation as biological control (Chapter 4). Predation by *A. baccharum* in laboratory experiments was observed only with *E. postvittana* eggs and therefore was left out of the preference trials. *F. auricularia* showed frequency-based prey selection of the two *E. postvittana* prey types when acceptability of the prey and electivity of the predators were taken in to consideration. However, *P. opilio* displayed a preference for eggs over larvae (Chapter 4).

### 6.2.2 Potential control of multiple pests

Prey preference is an important consideration when examining generalists. Depending on context, a preference for a target pest species can be desirable, as can frequency-dependent predation (Symondson et al., 2002). A lack of preference can be advantageous for biological control, as one pest becomes more prevalent, the relative predation rate increases (Symondson et al., 2002). In identifying the generalist predator species that could complement *D. tasmanica* in controlling *E. postvittana*, there was an opportunity to explore if any candidate species may also assist with management of a secondary pest. Management of *Ps. calceolariae* involves a substantial use of pesticide in New Zealand vineyards (Manktelow et al., 2005), and presents greater opportunities for pesticide reduction.

*A. baccharum*, *F. auricularia* and *P. opilio* showed an association with *E. postvittana* larvae and eggs as they were all observed predating on this pest (Chapter 2). The next step was to determine which of these candidate predator species for *E. postvittana* were capable of consuming the secondary pest, *Ps. calceolariae*. As part of establishing the maximum consumption rates of *E. postvittana* by the three generalist predator species in laboratory conditions, they were also



presented with *Ps. calceolariae* (Chapter 3). In the laboratory experiments, each of the predator species was presented with adult female *Ps. calceolariae* or *Ps. calceolariae* nymphs; only *F. auricularia* was observed consuming both of these prey types (Chapter 3). *P. opilio* consumed *P. calceolariae* nymphs, though at a significantly lower rate than did *F. auricularia*, whereas *A. baccharum* did not consume any *Ps. calceolariae* of either stage (Chapter 3). The *Ps. calceolariae* anti-predator defences of releasing ostiolar fluid or waxy secretions are two possible explanations the lack of predation of either prey type by *A. baccharum* and these defences in adult female *Ps. calceolariae* may have been enough to prevent predation by *P. opilio* (Daane et al., 2008).

Following on from the laboratory work, prey preference experiments were carried out between *Ps. calceolariae* nymphs with *E. postvittana* larvae or egg masses (Chapter 4). Only *F. auricularia* and *P. opilio* were included as no predation by *A. baccharum* was observed with any *Ps. calceolariae* prey types. No preference was shown between *Ps. calceolariae* and either *E. postvittana* prey type by either predator species (Chapter 4).

### 6.2.3 Inter-specific predator relationships

As mentioned above, one of the historical concerns of employing generalists in biological control is the risk of affecting other beneficial species. Schmitz (2007) highlighted that convergence of habitat use and hunting mode can indicate potential negative interactions between predator species. The three generalist predators, *P. opilio*, *F. auricularia* and *A. baccharum*, were already identified as having some niche overlap within the ecosystem as all were observed attacking *E. postvittana* within the same environment (Chapter 2). However, these relationships may not

always be negative ones, such as interference or intra-guild predation. Synergistic and additive pest predation relationships have been observed in assemblages of natural enemies (Sokol-Hessner and Schmitz, 2002; Snyder and Ives, 2003; Chailleux et al., 2013), including examples with *E. postvittana* in Australia and California, USA (Paull et al., 2012; Hogg et al., 2013). Using vineyard field cages, all combinations of *P. opilio*, *F. auricularia* and *A. baccharum* were presented with each of the prey types; *E. postvittana* larvae, *E. postvittana* egg masses and *P. calceolariae* nymphs (Chapter 5).

A variety of outcomes resulted from the interactions of different predator combination with the three different prey types (Chapter 5). Intra-guild predation was not observed in any of the predator combinations, though some antagonistic interactions did occur (Chapter 5). No predator species associated with a prey type or combination of predators across prey types showed a clear consistent interaction, with the sole exception of the assemblage of all three predator species. Across all three prey types, the three predator assemblages displayed an additive effect of pest removal, including *Ps. calceolariae* nymphs which *A. baccharum* had not shown any evidence of predation in any other work presented here (Chapter 5).

Two non-linear interactions occurred between predators with *E. postvittana* larval prey (Chapter 5). Both instances included *A. baccharum* paired with either of the other predator species and both relationships were synergistic for *E. postvittana* larvae. Three antagonistic interactions occurred, all three occurrences involved *F. auricularia* (Chapter 5). When this predator was presented with *E. postvittana* egg masses and paired with either *P. opilio* or *A. baccharum*, the predation risk to prey was reduced. The interaction between *P. opilio* and *F. auricularia* with *Ps. calceolariae* nymphs was also antagonistic and the predation rate was

reduced.

### 6.3 Conclusions

All three generalist predator species that were observed predating upon *E. postvittana* in Marlborough vineyards varied in their potential as CBC agents and of the secondary pest, *P. calceolarie*. No single predator species stood out clearly as the sole suitable candidate, nor could a species be ruled out of being included in management practices to complement the parasitoid *D. tasmanica*. The variation between how the predators interact with the pest and other predator species presents a range of options for application.

Organic management appeared to benefit functional invertebrate diversity and increase in the frequency of observations of predators predating upon *E. postvittana* from bait cards, yet this did not translate into higher removal rates of prey from the bait cards. This was consistent with other studies of biodiversity in respect of organic agriculture, which showed species diversity improved in organic production and beneficial arthropods were more abundant (Bengtsson et al., 2005; Winqvist et al., 2011; Sandhu et al., 2015). Functional diversity is seen as a more relevant measure of ecosystem services provided compared with species diversity, where the latter is assigned to functional groups with common functional traits and this comprises the functional diversity (Hooper et al., 2005; Wright et al., 2006; Wilby et al., 2005). Maintenance of high functional diversity, and species diversity within the functional groups, at a landscape scale provides insurance against losing ecosystem services through disturbances, possibly maintaining ecosystem stability and productivity, and decreasing invasion risk (Bengtsson et al., 2003;

Tscharntke et al., 2005; Crowder et al., 2010).

It is promising that functional diversity of invertebrate predators of organic management benefited relatively immediately, within three years of organic management and not yet certified organic (BioGro<sup>™</sup> New Zealand Ltd.), as the advantages of organic practices can increase over time (Seufert et al., 2012; Mondelaers et al., 2009; Birkhofer et al., 2008a). The survey of functional diversity was limited to vine canopy and under vine dwelling predators and was based on taxonomic groupings. Observing predation of a wider range of pest or prey species and the longer-term pest population stability could identify more relevant benefits to production derived from increased predator functional diversity (Crowder et al., 2010).

### 6.3.1 *A. baccharum*

The most abundant invertebrate predatory group was mites and *A. baccharum* was the most frequently observed predator attacking *E. postvittana* in vineyards. In the simplified laboratory arenas and vine canopy field cages, *A. baccharum* did not predate upon any *Ps. calceolariae* prey and very rarely on medium-sized *E. postvittana* in the field cages (Chapter 2; Chapter 3). However, medium-sized *E. postvittana* larvae were attacked when anchored on bait cards on vines and these predatory mites have been observed attacking first instar larvae (Chapter 2; Chapter 3) (Paull et al., 2012). *A. baccharum* still showed synergistic and additive relationships with these prey types when combined with *P. opilio* and *F. auricularia*, despite a lack of predation observations in isolation. An additive effect of the three predator assemblage was observed with *E. postvittana* larvae and *Ps. calceolariae* nymphs; this might be expected as their contribution to hypothesised and observed prey removal was non-existent or minimal. Importantly, *A. baccharum*

may play a role in mitigating antagonistic pairwise interactions between *P. opilio* and *F. auricularia* for both prey types, a potential advantage of incorporating *A. baccharum* in biological control of these pests.

*A. baccharum* has been recorded as a predator of *E. postvittana* and other tortricids in apple orchards (Baker, 1983; Cuthbertson and Murchie, 2005), as well as in other agricultural systems with pests such as mite, psyllid, leafhopper and aphid species (Cuthbertson et al., 2014; Duso et al., 2010). *A. baccharum* has been investigated as a CBC agent in a variety of other agricultural systems, though the means of managing them are limited (Cuthbertson et al., 2014). Methods of promoting the efficacy of this mite have been restricted to minimising pesticide applications and correct identification to avoid it being mistaken as pest mite species (Cuthbertson and Murchie, 2010). Encouragingly, this predator species is compatible with fungicides such as sulphur, the most widely used pesticide in New Zealand vineyards, and shows a tolerance to some insecticides (Cuthbertson et al., 2014; Manktelow et al., 2005). Methods that have been applied to other generalist predatory mites may be applicable to *A. baccharum* if there are similarities in habitat use (McMurtry et al., 2013). Supplementary provisioning of Rhodes grass (*Chloris gayana*) pollen for *Euseius scutalis* (Acari: Phytoseiidae) can improve control of perseus mite, *Oligonychus perseae* (Acari: Tetranychidae), in avocado orchards and citrus rust mite, *Phyllocoptruta oleivora* (Acari: Eriophyidae), in citrus orchards (Maoz et al., 2011, 2014). However, an approach specific to *A. baccharum* would need to be investigated as it is unlikely a practice using plant-based food supplementation (i.e. pollen) would work because Phytoseiid mites are often omnivorous and Anystid mites predatory (Adar et al., 2014).

Paull et al. (2012) looked explicitly at the interaction between *D. tasmanica*

and *A. baccharum* in relation to the removal of *E. postvittana* larvae for South Australian vineyards. A short-term synergism was facilitated by the action of *D. tasmanica* parasitism inducing *E. postvittana* larvae to leave their hibernaculum (silken refuge), making them prone to predation by *A. baccharum* (Paull et al., 2012). However, parasitoid recruitment was expected to decrease and reduce long-term pest control, because increased predation was reliant on parasitism (Paull et al., 2012; Hogg et al., 2013).

*A. baccharum* was the predominant predator in Marlborough vineyards and a potentially mediated the antagonistic interactions of *P. opilio* and *F. auricularia* with *Ps. calceolariae* nymphs and *E. postvittana* larvae. Perhaps the role of *A. baccharum* for biological control may not need to be increased but maintained to complement other natural enemies. However, inclusion of *A. baccharum* in future experiments investigating generalist predators for management of *E. postvittana* and *P. calceolariae* will be important as it cannot be ruled out as a stand-alone biological control agent.

### **6.3.2 *F. auricularia***

*F. auricularia* showed promise in the preceding chapters as a voracious predator of all prey presented to it. This predator species had the highest predation rate of all prey types in the laboratory and vineyard field cages and was comparatively frequently observed in surveys in vineyards (Chapter 2; Chapter 3; Chapter 4; Chapter 5). Not only did this species consume *E. postvittana* eggs and larvae and *Ps. calceolariae* nymphs, but it was the only species to predate upon adult female *Ps. calceolariae* (Chapter 3; Chapter 4; Chapter 5).

The potential advantages of *F. auricularia* attacking more prey and a wider range of prey types has to be weighed against the negative interactions with other predator species of *E. postvittana*. All antagonistic inter-predator relationships observed in Chapter 5 involved *F. auricularia*; predation of *E. postvittana* eggs and *Ps. calceolariae* nymphs was reduced when combined with *P. opilio*, as was *E. postvittana* egg predation with *A. baccharum*. One synergistic interaction occurred, with *F. auricularia* and *A. baccharum* enhancing predation risk of *E. postvittana* larvae. No preference by *F. auricularia* was observed between *E. postvittana* eggs and larvae and *Ps. calceolariae* nymphs, suggesting frequency-dependent prey selection.

*F. auricularia* has been previously identified as a predator of *E. postvittana* and a variety of other pest species including *Pseudococcus spp.* (Moerkens et al., 2009; Danthanarayana, 1983; Frank et al., 2007; Suckling et al., 2006; He et al., 2008; Solomon et al., 2000; Daane et al., 2008). Observations of *F. auricularia* being able to enter the hibernaculum of *E. postvittana* would be an advantage as it reduces the security of the pest's refuge (Danthanarayana, 1983). A concern is possible direct damage to fruit by *F. auricularia*, as it has been considered a pest of soft fleshed fruit and degrade grape bunches with berry damage and frass affecting wine quality (Lordan et al., 2014; Burnip et al., 2002). In apple orchards, *F. auricularia* have been found with fruit in their gut but this is likely to be from feeding at previously wounded fruit, not the primary cause of fruit damage (Solomon et al., 2000).

Moerkens et al. (2009) investigated the factors limiting *F. auricularia* populations in Belgian apple and pear orchards to identify practices for promoting the species as a biological control agent. Supplementary plantings, such as Aus-

tralian perennial grasses, were suggested as a means to assist *F. auricularia* with food and habitat complexity to increase the capacity of the environment, reducing competition and improving over wintering habitat (Moerkens et al., 2009; Danne et al., 2010; Gobin et al., 2006). Stem and canopy complexity can play a role in encouraging residence in the canopy environment (Moerkens et al., 2009). Providing refuge with straw mulch under vines or tubes around trunks (i.e. corrugated cardboard) are practices that could improve *F. auricularia* pest management, and the aggregative behaviour of *F. auricularia* could make artificial refuges useful for monitoring of populations and a practicable method of moving applying predators where needed (Suckling et al., 2006; Lordan et al., 2014). Under-vine tilling and the use of pesticides, particularly broad spectrum, are harmful to *F. auricularia* populations to the detriment of pest predation (Logan et al., 2011; Sharley et al., 2008). However, developments with phenological day-degree models could minimise the impact of under- or between-vine soil tillage and necessary agro-chemical applications (Moerkens et al., 2011).

*F. auricularia* merits further investigation because of its voracity for all the prey types presented. A focus of research into *F. auricularia* in biological control has been to improve over-wintering capability, which would improve early-season pest control to complement *D. tasmanica* (Moerkens et al., 2011). Employing phenological day-degree models would help integrate *F. auricularia* with supplementary plantings for *D. tasmanica* to maximise impacts and minimise any impacts from necessary agro-chemical applications Moerkens et al. (2011). However, it would be prudent to address any potential fruit or vine damage that may occur and antagonistic relationships with *P. opilio* or *A. baccarum*.



### 6.3.3 *P. opilio*

*P. opilio* showed capability as predator of both *E. postvittana* and *Ps. calceolariae* and was one of the most widespread predators in the Marlborough vineyards. While *P. opilio* did not predate on adult female *Ps. calceolariae*, they were capable of eating nymphs along with *E. postvittana* eggs and larvae. The only display of prey preference shown was for *E. postvittana* eggs over *E. postvittana* larvae by *P. opilio*. Frequency dependence is desirable for controlling both pest species; however this preference was between developmental stages of a species and no preference was observed between *Ps. calceolariae* nymphs and either *E. postvittana* prey type.

Promotion of *P. opilio* at the expense of one of the other predator species could complicate pest management. *P. opilio* showed a non-linear interaction with another predator for each of the three prey types in vineyard cages. A synergistic relationship occurred with *A. baccharum* to enhance the predation risk for *E. postvittana* larvae. However, for *E. postvittana* egg masses and *Ps. calceolariae* nymphs, *P. opilio* and *F. auriculariae* interacted negatively and the predation risk was reduced. This would suggest if *P. opilio* were employed to manage both pest species, then the presence of the two alternative complementary predators should be maintained.

The ubiquity and generalist diet of *P. opilio* has to its appeal as a biological control agent in other systems, as a predator of *E. postvittana* and other pest species (Frank et al., 2007; Danthanarayana, 1983; Merfield et al., 2004; Allard and Yeorgan, 2005). A literature search found no examples of *P. opilio* predating on *Ps. calceolariae*, suggesting this association had not previously been recorded. Previous research has investigated the prospect of using *P. opilio* as a biological

control agent in agricultural systems, though there were no examples found of actively managing this predator species to control pests (Vink et al., 2004; Allard and Yeargan, 2005; Merfield et al., 2004).

A potential advantage of *P. opilio* was the preference for *E. postvittana* eggs over larvae. A lack of preference for parasitised *E. postvittana* larvae has been suggested to mitigate an antagonistic relationship between a generalist predator and a parasitoid (Hogg et al., 2013). A preference for eggs is encouraging for *P. opilio* to complement the larval parasitoid *D. tasmanica* as there may be a reduced overlap in predation and parasitism, indicating a theoretical synergism (Hogg et al., 2013; Schmitz, 2007).

Based on Merfield et al. (2004), it was posited that *A. baccharum* and *P. opilio* might have a synergistic predator relationship for *E. postvittana* eggs. Predation of brown blowfly, *Calliphora stygia* (Diptera: Calliphoridae) eggs by mites, *Bal-austium* species (Acari: Erythraeidae), stimulated increased egg predation by *P. opilio* (Merfield et al., 2004). This did not occur in the *A. baccharum* and *P. opilio* relationship which was additive for *E. postvittana* egg removal (Chapter 5).

In order for *P. opilio* to become part of the pest control “tool box” of vineyard managers, there are concerns to be addressed before the potential advantages of this predator species can be used. The negative interactions and seasonal variation of predation in the vineyards are issues that could be remedied through management. For example, maintenance of *A. baccharum* may minimise the antagonistic interactions with *F. auricularia*. However, consuming both pest species and the theoretical lack of antagonism with *D. tasmanica* still makes *P. opilio* a prospective biological control agent.

## 6.4 Future research

The preceding chapters presented three generalist predator species that could potentially augment pest control in vineyards. There is still further research required before reaching a stage where the benefits to crop production by these potential biological control agents can be measured and management practices developed. While the ecosystem services provided may increase from CBC management, the final proof of a successful practice is the improvement of crop yield and quality (Symondson et al., 2002).

A necessary step in advancing these potential biological agents is to examine how they interact with the existing CBC agent, *D. tasmanica*. This would not be limited to examining linear and non-linear relationships, as in Chapter 5, though this would be important. Hogg et al. (2013) highlighted the possible importance of detecting preference or lack thereof for parasitised larvae which can impact on the long-term sustainability of the parasitoid population and effective pest control. An immediate antagonistic relationship between *M. ictericus* and *C. mildeia* was beneficial to *E. postvittana* over a longer period as there was no preference for parasitised larvae (Hogg et al., 2013). Whereas, modelling suggested the synergistic relationship between *A. baccarum* and *D. tasmanica* would be detrimental to the parasitoid long-term and reduce *E. postvittana* control because parasitism was necessary to facilitate the increased predation (Paull et al., 2012). Examining the interactions between the natural enemies and preferences between prey types over longer time-scales and in arenas less restrictive than those in Chapters 3, 4, and 5 would help to improve the understanding of the appropriateness of the predator species. Additionally, other beneficial and desired species within the vineyard

environment should be included into expanded research, as the relationship and impact with these species would have to be considered, including the grapevines. *F. auricularia* in particular may lead to cause for concern regarding vine and berry damage (Lordan et al., 2014), and quantifying any possible damage would help vineyard managers assess the cost-benefit of using this predator species.

Recently developed techniques, such as molecular gut-content analysis, could help to identify the range of species that the candidate predator species attack and any possible crop damage (Symondson and Harwood, 2014; Boyer et al., 2012; Lefort et al., 2012). These same techniques could also be used to test spider species for consumption of either *E. postvittana* or *Ps. calceolariae*. Spider species have been identified and investigated as biological control agents of *E. postvittana*, including in vineyards (Hogg et al., 2013, 2014; Baker, 1983; Suckling and Brockerhoff, 2010). The lack of observations of spider species predating on *E. postvittana*, despite occurring in other environments (Baker, 1983; Hogg et al., 2013, 2014; Danthanarayana, 1983), may be due to the monitoring method used in Chapter 2. The high diversity of spider-hunting modes and relatively high abundance in vineyards could be a useful tool for pest management in vineyards (Riechert, 1999; Riechert and Bishop, 1990; Costello and Daane, 1999). The association of *P. opilio* predating on *Ps. calceolariae* was apparently not previously observed; this may be because this does not occur or is very rare in open vineyard systems. Using molecular gut-content analysis or similar techniques would detect if *Ps. calceolariae* predation does occur in more natural vineyard settings. Inclusion of *Ps. longispinus* in this molecular work would help to confirm if observations of predation with *P. opilio* and *F. auricularia* were consistent with both mealybug species.

A final stage in developing the CBC protocol is developing a suitable practice of promoting the desired generalist predator species. Defining the predator species' service providing units (SPU) that are necessary to provide a applicable protocol for vineyard managers is important. An SPU is a unit of a population that provides an ecosystem service over a spatial or temporal range (Luck et al., 2003). This requires expanding on the examination of individuals to how spatial and temporal population dynamics of the desired predator species in vineyards relate to pest management (Luck et al., 2003). Supplementary plantings and habitat complexity have been suggested as potential practices to encourage *F. auricularia* as biological control but less research has been carried out on promoting *A. baccharum* and *P. opilio* (Moerkens et al., 2009). Care would need to be taken that any practice does not benefit *E. postvittana*, *Ps. calceolariae*, *Ps. longispinus* or other vineyard pest species as well. Supplementary plantings would appeal, as this practice is currently used to promote *D. tasmanica* effectiveness and may be simpler to add into a vineyard pest management scheme (Berndt et al., 2002; Berndt and Wratten, 2005; Berndt et al., 2006; Irvin et al., 2006).

The work on the previous chapters constructed a base for further research by identifying and developing a generalist predator species that could complement *D. tasmanica* for controlling *E. postvittana* and *Ps. calceolariae* in vineyards. Theory and examples have highlighted the possibilities combining generalist and specialist natural enemies to improve pest control (Schmitz, 2007; Ives et al., 2005; Hogg et al., 2013; Chailleux et al., 2013; Long and Finke, 2014). Recent publications have examined generalist predators to complement parasitoids for controlling *E. postvittana* in Australia and California, USA, highlighting that there is interest in incorporating these ideas into biological control of this pest (Hogg et al., 2013; Paull et al., 2012). While *P. opilio*, *F. auricularia* and *A. baccharum* have varying

advantages that merit further investigation, there is also possible limitations that need to be addressed through further research.

# References

- Abrams, P. A. (1993). Why predation rate should not be proportional to predator density. *Ecology*, 74(3):726–733.
- Adar, E., Inbar, M., Gal, S., Issman, L., and Palevsky, E. (2014). Plant cell piercing by a predatory mite: evidence and implications. *Experimental and Applied Acarology*, 65(2):181–193.
- Aktar, W., Sengupta, D., and Chowdhury, A. (2009). Impact of pesticides use in agriculture: their benefits and hazards. *Interdisciplinary Toxicology*, 2(1):1–12.
- Alexandratos, N. (1999). World food and agriculture: outlook for the medium and longer term. *Proceedings of the National Academy of Sciences of the United States of America*, 96(11):5908–5914.
- Allard, C. M. and Yeargan, K. V. (2005). Effect of diet on development and reproduction of the harvestman *Phalangium opilio* (Opiliones: Phalangidae). *Environmental Entomology*, 34(1):6–13.
- Altieri, M. A. (1999). The ecological role of biodiversity in agroecosystems. *Agriculture, Ecosystems and Environment*, 74:19–31.
- Altieri, M. A., Ponti, L., and Nicholls, C. I. (2005). Manipulating vineyard biodiversity for improved insect pest management: case studies from Northern California. *International Journal of Biodiversity Science and Management*, 1(4):191–203.
- Anderson, M. S. R. (2012). *The effect of landscape- and local-scale non-crop vegetation on arthropod pests and predators in vineyards*. PhD thesis, Lincoln University, New Zealand.
- Bailey, P. T., Ferguson, K. L., McMahon, R., and Wicks, T. J. (1997). Transmission of *Botrytis cinerea* by light brown apple moth larvae on grapes. *Australian Journal of Grape and Wine Research*, 3(2):90–94.
- Baker, R. T. (1983). Predation of leafroller larvae by spiders and mites. *Weta*, 6(1):22–23.

- Bale, J. S., van Lenteren, J. C., and Bigler, F. (2008). Biological control and sustainable food production. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1492):761–776.
- Barata, A., Malfeito-Ferreira, M., and Loureiro, V. (2012). The microbial ecology of wine grape berries. *International Journal of Food Microbiology*, 153(3):243–59.
- Begum, M., Gurr, G. M., Wratten, S. D., Hedberg, P. R., and Nicol, H. I. (2004). The effect of floral nectar on the grapevine leafroller parasitoid *Trichogramma carvae*. *International Journal of Ecology and Environmental Sciences*, 30:3–12.
- Begum, M., Gurr, G. M., Wratten, S. D., Hedberg, P. R., and Nicol, H. I. (2006). Using selective food plants to maximize biological control of vineyard pests. *Journal of Applied Ecology*, 43(3):547–554.
- Bell, V. A., Bonfiglioli, R. G. E., Walker, J. T. S., Lo, P. L., Mackay, J. F., and McGregor, S. E. (2009). Grapevine leafroll-associated virus 3 persistence in vitis vinifera remnant roots. *Journal of Plant Pathology*, 91:527–533.
- Bell, V. A., Brightwell, R. J., and Lester, P. J. (2006). Increasing vineyard floral resources may not enhance localised biological control of the leafroller *Epiphyas postvittana* (Lepidoptera: Tortricidae) by *Dolichogenidea* spp. (Hymenoptera: Braconidae) parasitoids. *Biocontrol Science and Technology*, 16(10):1031–1042.
- Bengtsson, J., Ahnström, J., and Weibull, A.-C. (2005). The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *Journal of Applied Ecology*, 42(2):261–269.
- Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F., and Nyström, M. (2003). Reserves, resilience and dynamic landscapes. *AMBIO: A Journal of the Human Environment*, 32(6):389–396.
- Berndt, L. A. and Wratten, S. D. (2005). Effects of alyssum flowers on the longevity, fecundity, and sex ratio of the leafroller parasitoid *Dolichogenidea tasmanica*. *Biological Control*, 32:65–69.
- Berndt, L. A., Wratten, S. D., and Hassan, P. G. (2002). Effects of buckwheat flowers on leafroller (Lepidoptera: Tortricidae) parasitoids in a New Zealand vineyard. *Agricultural and Forest Entomology*, 4(1):39–45.
- Berndt, L. A., Wratten, S. D., and Scarratt, S. L. (2006). The influence of floral resource subsidies on parasitism rates of leafrollers (Lepidoptera: Tortricidae) in New Zealand vineyards. *Biological Control*, 37:50–55.
- Birkhofer, K., Bezemer, T. M., Bloem, J., Bonkowski, M., Christensen, S., Dubois, D., Ekelund, F., Fließbach, A., Gunst, L., and Hedlund, K. (2008a). Long-term organic farming fosters below and above ground biota: Implications for



- soil quality, biological control and productivity. *Soil Biology and Biochemistry*, 40(9):2297–2308.
- Birkhofer, K., Gavish-Regev, E., Endlweber, K., Lubin, Y. D., von Berg, K., Wise, D. H., and Scheu, S. (2008b). Cursorial spiders retard initial aphid population growth at low densities in winter wheat. *Bulletin of Entomological Research*, 98(3):249–255.
- Bisson, L. F., Waterhouse, A. L., Ebeler, S. E., Walker, M. A., and Lapsley, J. T. (2002). The present and future of the international wine industry. *Nature*, 418(6898):696–699.
- Bureau de Roince, C., Lavigne, C., Mandrin, J.-F., Rollard, C., and Symondson, W. O. C. (2013). Early-season predation on aphids by winter-active spiders in apple orchards revealed by diagnostic PCR. *Bulletin of Entomological Research*, 103:148–154.
- Boyer, S., Brown, S. D. J., Collins, R. A., Cruickshank, R. H., Lefort, M. C., Malumbres-Olarte, J., and Wratten, S. D. (2012). Sliding window analyses for optimal selection of mini-barcodes, and application to 454-pyrosequencing for specimen identification from degraded DNA. *PLoS ONE*, 7(5):1–8.
- Bramley, R. G. V., Trought, M. C. T., and Praat, J. P. (2011). Vineyard variability in Marlborough, New Zealand: characterising variation in vineyard performance and options for the implementation of precision viticulture. *Australian Journal of Grape and Wine Research*, 17(1):72–78.
- Bray, D. B., Sánchez, J. L. P., and Murphy, E. C. (2002). Social dimensions of organic coffee production in Mexico: lessons for eco-labeling initiatives. *Society and Natural Resources: An International Journal*, 15(5):429 – 446.
- Bristowe, W. S. (1949). The distribution of harvestmen (Phalangida) in Great Britain and Ireland, with notes on their names, enemies and food. *Journal of Animal Ecology*, 18(1):100–114.
- Brown, J. S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology*, 22(1):37–47.
- Brussaard, L. (2013). Biodiversity and ecosystem functioning in soil. *Ambio*, 26(8):563–570.
- Burnip, G. M., Daly, J. M., Hackett, J. K., and Suckling, D. M. (2002). European earwig phenology and effect of understorey management on population estimation. *New Zealand Plant Protection*, 395:390–395.
- Byrnes, J. E. and Stachowicz, J. J. (2009). The consequences of consumer diversity loss: different answers from different experimental designs. *Ecology*, 90(10):2879–2888.

- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., and Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, 489(7401):59–67.
- Cardinale, B. J., Harvey, C. T., Gross, K., and Ives, A. R. (2003). Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecology Letters*, 6(9):857–865.
- Carrillo, D. and Peña, J. E. (2012). Prey-stage preferences and functional and numerical responses of *Amblyseius largoensis* (Acari: Phytoseiidae) to *Raoiella indica* (Acari: Tenuipalpidae). *Experimental and Applied Acarology*, 57:361–372.
- Caspari, H. W., Neal, S., and Naylor, A. (1997). Cover crop management in vineyards to enhance deficit irrigation in a humid climate. In Chantzoulakis, K. S., editor, *2nd International Symposium on Irrigation of Horticultural Crops*, volume 1, pages 313–320.
- Chailleux, A., Bearez, P., Pizzol, J., Amiens-Desneux, E., Ramirez-Romero, R., and Desneux, N. (2013). Potential for combined use of parasitoids and generalist predators for biological control of the key invasive tomato pest *Tuta absoluta*. *Journal of Pest Science*, 86:533–541.
- Chailleux, A., Mohl, E. K., Teixeira Alves, M., Messelink, G. J., and Desneux, N. (2014). Natural enemy-mediated indirect interactions among prey species: potential for enhancing biocontrol services in agroecosystems. *Pest Management Science*, 70(12):1769–1779.
- Chang, G. C. and Kareiva, P. (1999). The case for indigenous generalists in biological control. In Hawkins, B. A. and Cornell, H. V., editors, *Theoretical Approaches to Biological Control*, chapter 6, pages 103–115. Cambridge University Press, Port Chester, NY, USA.
- Charles, J. G. (1981). Distribution and life history of the longtailed mealybug *Pseudococcus longispinus* (Homoptera: Pseudococcidae), in Auckland vineyards. *New Zealand Journal of Zoology*, 8:285–293.
- Charles, J. G. (1982). Economic damage and preliminary economic thresholds for mealybugs (*Pseudococcus longispinus* T.-T.) in Auckland vineyards. *New Zealand Journal of Agricultural Research*, 25:415–420.
- Charles, J. G. (1985). *Diadiplosis koebelei* Koebele (Diptera: Cecidomyiidae), a predator of *Pseudococcus longispinus* T.-T. (Homoptera: Pseudococcidae), newly recorded from New Zealand. *New Zealand Journal of Zoology*, 12:331–333.

- Charles, J. G. (1993). A survey of mealybugs and their natural enemies in horticultural crops in North Island, New Zealand, with implications for biological control. *Biocontrol Science and Technology*, 3(4):405–418.
- Charles, J. G., Bell, V. A., Lo, P. L., Cole, L. M., and Chhagan, A. (2010). Mealybugs (Hemiptera: Pseudococcidae) and their natural enemies in New Zealand vineyards from 1993-2009. *New Zealand Entomologist*, 33(1):84–91.
- Charles, J. G., Cohen, D., Walker, J. T. S., Forgie, S. A., Bell, V. A., and Breen, K. C. (2006). A review of the ecology of Grapevine Leafroll associated Virus type 3 (GLRaV-3). *New Zealand Plant Protection*, 59:330–337.
- Charles, J. G., Froud, K. J., van den Brink, R., and Allan, D. J. (2009). Mealybugs and the spread of Grapevine Leafroll-associated Virus 3 (GLRaV-3) in a New Zealand vineyard. *Australasian Plant Pathology*, 38:576.
- Charles, J. G., Walker, J. T. S., and White, V. (1996). Leafroller phenology and parasitism in Hawkes Bay, New Zealand, canefruit gardens. *New Zealand Journal of Crop and Horticultural Science*, 24:123–131.
- Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical population biology*, 9(2):129–136.
- Choueiri, E., Boscia, D., Digiaro, M., Castellano, M. A., and Martelli, G. P. (1996). Some properties of a hitherto undescribed filamentous virus of the grapevine. *Vitis*, 35:91–93.
- Colfer, R. G. and Rosenheim, J. A. (2001). Predation on immature parasitoids and its impact on aphid suppression. *Oecologia*, 126:292–304.
- Collier, T. and van Steenwyk, R. A. (2004). A critical evaluation of augmentative biological control. *Biological Control*, 31:245–256.
- Collier, T. and van Steenwyk, R. A. (2006). How to make a convincing case for augmentative biological control. *Biological Control*, 39:119–120.
- Colucci, M. S., Bork, H., and Topp, E. (2001). Persistence of estrogenic hormones in agricultural soils: I.  $17\beta$ -estradiol and estrone. *Journal of Environmental Quality*, 17:2070–2076.
- Costanza, R., D’Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O’Neill, R. V., Paruelo, J., Raskin, R. G., Sutton, P., and van den Belt, M. (1997). The value of the world’s ecosystem services and natural capital. *Nature*, 387(6630):253–260.
- Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S. J., Kubiszewski, I., Farber, S., and Turner, R. K. (2014). Changes in the global value of ecosystem services. *Global Environmental Change*, 26:152–158.

- Costello, M. J. and Daane, K. M. (1999). Abundance of spiders and insect predators on grapes in central California. *Journal of Arachnology*, 27(2):531–538.
- Costello, M. J. and Daane, K. M. (2005). Day versus night sampling for spiders in vineyards. *Journal of Arachnology*, 33(1):25–32.
- Credi, R. and Babini, A. R. (1997). Effects of virus and virus-like injections on growth, yield, and fruit quality of Albana and Trebbiano Romagnolo Grapevines. *American Journal of Enology and Viticulture*, 48:7–12.
- Crowder, D. W., Northfield, T. D., Strand, M. R., and Snyder, W. E. (2010). Organic agriculture promotes evenness and natural pest control. *Nature*, 466(7302):109–112.
- Cullen, R., Warner, K. D., Jonsson, M., and Wratten, S. D. (2008). Economics and adoption of conservation biological control. *Biological Control*, 45(2):272–280.
- Cuthbertson, A. G. S., Fleming, C. C., and Murchie, A. K. (2003). Detection of *Rhopalosiphum insertum* (apple-grass aphid) predation by the predatory mite *Anystis baccarum* using molecular gut analysis. *Agricultural and Forest Entomology*, 5(3):219–225.
- Cuthbertson, A. G. S. and Murchie, A. K. (2003). The impact of fungicides to control apple scab (*Venturia inaequalis*) on the predatory mite *Anystis baccarum* and its prey *Aculus schlechtendali* (apple rust mite) in Northern Ireland Bramley orchards. *Crop Protection*, 22(9):1125–1130.
- Cuthbertson, A. G. S. and Murchie, A. K. (2004). The phenology, oviposition and feeding rate of *Anystis baccarum*, a predatory mite in Bramley apple orchards in Northern Ireland. *Experimental and Applied Acarology*, 34:367–373.
- Cuthbertson, A. G. S. and Murchie, A. K. (2005). Environmental monitoring of *Archips podana* (fruit tree tortrix moth) in Bramley apple orchards in Northern Ireland. *International Journal of Environment Science and Technology*, 2(2):101–104.
- Cuthbertson, A. G. S. and Murchie, A. K. (2010). Ecological benefits of *Anystis baccarum* in an orchard ecosystem and the need for its conservation. *International Journal of Environment Science and Technology*, 7(4):807–813.
- Cuthbertson, A. G. S., Qiu, B.-L., and Murchie, A. (2014). *Anystis baccarum*: an important generalist predatory mite to be considered in apple orchard pest management strategies. *Insects*, 5:615–628.
- Daane, K. M., Almeida, R. P. P., Bell, V. A., Walker, J. T. S., Botton, M., Fallahzadeh, M., Mani, M., Miano, J. L., Sforza, R., Walton, V. M., and Zaviezo, T. (2012). Biology and management of mealybugs in vineyards. In Bostanian, N. J., Vincent, C., and Isaacs, R., editors, *Arthropod Management in Vineyards*, chapter 12, page 37. Springer, Netherlands.

- Daane, K. M., Cooper, M. L., Triapitsyn, S. V., Walton, V. M., Yokota, G. Y., Haviland, D. R., Bentley, W. J., Godfrey, K., and Wunderlich, L. R. (2008). Vineyard managers and researchers seek sustainable solutions for mealybugs, a changing pest complex. *California Agriculture*, 62(4):167–176.
- Daane, K. M., Middleton, M. C., Sforza, R., Cooper, M. L., Walton, V. M., Walsh, D. B., Zaviezo, T., and Almeida, R. P. P. (2011). Development of a multiplex PCR for identification of vineyard mealybugs. *Environmental Entomology*, 40(6):1595–1603.
- Daane, K. M., Sime, K. R., Fallon, J., and Cooper, M. L. (2007). Impacts of Argentine ants on mealybugs and their natural enemies in California’s coastal vineyards. *Ecological Entomology*, 32(6):583–596.
- Danne, A., Thomson, L. J., Sharley, D. J., Penfold, C. M., and Hoffmann, A. A. (2010). Effects of native grass cover crops on beneficial and pest invertebrates in Australian vineyards. *Environmental Entomology*, 39(3):970–978.
- Danthanarayana, W. (1975). The bionomics, distribution and host range *Epiphyas postvittana* (Walk.) (Tortricidae). *Australian Journal of Zoology*, 23:419–437.
- Danthanarayana, W. (1983). Population Ecology of the Light Brown Apple Moth, *Epiphyas postvittana* (Lepidoptera: Tortricidae). *Journal of Animal Ecology*, 52(1):1–33.
- Delate, K., Mckern, A., Turnbull, R., Walker, J. T. S., Volz, R., White, A., Bus, V., Rogers, D., Cole, L., How, N., Guernsey, S., and Johnston, J. (2008). Organic apple production in two humid regions: comparing progress in pest management strategies in Iowa and New Zealand. *HortScience*, 43(1):12–21.
- Dunne, J. A., Williams, R. J., and Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, 5:558–567.
- Duso, C., Castagnoli, M., Simoni, S., and Angeli, G. (2010). The impact of eriophyoids on crops: Recent issues on *Aculus schlechtendali*, *Calepitrimerus vitis* and *Aculops lycopersici*. *Experimental and Applied Acarology*, 51:151–168.
- Eber, S. (2001). Multitrophic interactions: the population dynamics of spatially structured plant-herbivore-parasitoid systems. *Basic and Applied Ecology*, 2(1):27–33.
- Edgar, A. L. (1966). Phalangida of the Great Lakes region. *American Midland Naturalist*, 75(2):347–366.
- Eilenberg, J., Hajek, A., and Lomer, C. (2001). Suggestions for unifying the terminology in biological control. *BioControl*, 46(4):387–400.

- El-Sayed, A. M., Unelius, C. R., Twidle, A., Mitchell, V., Manning, L. A., Cole, L., Suckling, D. M., Flores, M. F., Zaviezo, T., and Bergmann, J. (2010). Chrysanthemyl 2-acetoxy-3-methylbutanoate: the sex pheromone of the citrophilous mealybug, *Pseudococcus calceolariae*. *Tetrahedron Letters*, 51:1075–1078.
- Eskenazi, B., Harley, K., Bradman, A., Weltzien, E., Jewell, N. P., Barr, D. B., Furlong, C. E., and Holland, N. T. (2004). Association of in utero organophosphate pesticide exposure and fetal growth and length of gestation in an agricultural population. *Environmental Health Perspectives*, 112(10):1116–1124.
- Fantail Viticulture Consultants (2013). New Zealand Winegrowers vineyard spray schedule 2013/2014. Technical Report July, New Zealand Winegrowers, Auckland, New Zealand.
- Fantinou, A. A., Perdikis, D. C., Maselou, D. A., and Lambropoulos, P. D. (2008). Prey killing without consumption: does *Macrolophus pygmaeus* show adaptive foraging behaviour? *Biological Control*, 47(2):187–193.
- Finke, D. L. and Snyder, W. E. (2008). Niche partitioning increases resource exploitation by diverse communities. *Science*, 321(5895):1488–1490.
- Forbes, S. L., Cullen, R., Cohen, D. A., Wratten, S. D., and Fountain, J. (2011). Food and wine production practices: an analysis of consumer views. *Journal of Wine Research*, 22(1):79–86.
- Fountain, J. and Tompkins, J. M. L. (2011). The potential of wine tourism experiences to impart knowledge of sustainable practices: the case of the Greening Waipara biodiversity trails. In *6th AWBR International Conference*, pages 9–10, Bordeaux, France.
- Frank, S. D., Wratten, S. D., Sandhu, H. S., and Shrewsbury, P. M. (2007). Video analysis to determine how habitat strata affects predator diversity and predation of *Epiphyas postvittana* (Lepidoptera: Tortricidae) in a vineyard. *Biological Control*, 41(2):230–236.
- Gabriel, D., Sait, S. M., Kunin, W. E., and Benton, T. G. (2013). Food production vs. biodiversity: comparing organic and conventional agriculture. *Journal of Applied Ecology*, 50:355–364.
- Gardiner, M. M., Landis, D. A., Gratton, C., DiFonzo, C. D., O’Neal, M., Chacon, J. M., Wayo, M. T., Schmidt, N. P., Mueller, E. E., and Heimpel, G. E. (2009). Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. *Ecological Applications*, 19(1):143–154.
- Garnett, T., Appleby, M. C., Balmford, A., Bateman, I. J., Benton, T. G., Bloomer, P., Burlingame, B., Dawkins, M., Dolan, L., Fraser, D., Herrero, M., Hoffmann, I., Smith, P., Thornton, P. K., Toulmin, C., Vermeulen, S. J., and

- Godfray, H. C. J. (2013). Sustainable intensification in agriculture: premises and policies. *Science*, 341:33–34.
- Geiger, F., Bengtsson, J., Berendse, F., Weisser, W. W., Emmerson, M., Morales, M. B., Ceryngier, P., Liira, J., Tscharnkte, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L. W., Dennis, C., Palmer, C., Oñate, J. J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P. W., and Inchausti, P. (2010). Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology*, 11(2):97–105.
- Gerland, P., Raftery, A. E., Sevčiková, H., Li, N., Gu, D., Spoorenberg, T., Alkema, L., Fosdick, B. K., Chunn, J., Lalic, N., Bay, G., Buettner, T., Heilig, G. K., and Wilmoth, J. (2014). World population stabilization unlikely this century. *Science*, 346(6206):234–237.
- Gibson, R. H., Pearce, S., Morris, R. J., Symondson, W. O. C., and Memmott, J. (2007). Plant diversity and land use under organic and conventional agriculture: a whole-farm approach. *Journal of Applied Ecology*, 44(4):792–803.
- Girolami, V., Mazzon, L., Squartini, A., Mori, N., Marzaro, M., di Bernardo, A., Greatti, M., Giorio, C., and Tapparo, A. (2009). Translocation of neonicotinoid insecticides from coated seeds to seedling guttation drops: a novel way of intoxication for bees. *Journal of Economic Entomology*, 102(5):1808–1815.
- Gobin, B., Marien, A., Davis, S., and Leirs, H. (2006). Enhancing earwig populations in Belgian orchards. *Communications in Applied and Agricultural Biological Sciences*, 71(2):269–274.
- Godfray, H. C. J., Beddington, J. R., Crute, I. R., Haddad, L., Lawrence, D., Muir, J. F., Pretty, J., Robinson, S., Thomas, S. M., and Toulmin, C. (2010). Food security: the challenge of feeding 9 billion people. *Science*, 327(5967):812–818.
- Greathead, D. J. and Greathead, A. H. (1992). Biological control of insect pests by insect parasitoids and predators: the BIOCAT database. *Biocontrol News and Information*, 13(4):61N–68N.
- Griffen, B. D. (2006). Detecting emergent effects of multiple predator species. *Oecologia*, 148(4):702–709.
- Griffen, B. D. and Byers, J. E. (2006). Intraguild predation reduces redundancy of predator. *Journal of Animal Ecology*, 75:959–966.
- Gurr, G. M. and Nicol, H. I. (2000). Effect of food on longevity of adults of *Trichogramma carverae* Oatman and Pinto and *Trichogramma brassicae* Bezdenko (Hymenoptera: Trichogrammatidae). *Australian Journal of Entomology*, 39(3):185–187.

- Gurr, G. M., Scarratt, S. L., Wratten, S. D., Berndt, L. A., and Irvin, N. A. (2004). Ecological engineering, habitat manipulation and pest management. In Gurr, G. M., Wratten, S. D., and Altieri, M. A., editors, *Ecological Engineering for Pest Management: Advances in Habitat Manipulation for Arthropods*, chapter Chapter 2, pages 1–12. CABI Publishing, Wallingford, UK.
- Gurr, G. M. and Wratten, S. D. (1999). FORUM 'Integrated biological control': a proposal for enhancing success in biological control. *International Journal of Pest Management*, 45(2):81–84.
- Gurr, G. M., Wratten, S. D., and Luna, J. M. (2003). Multi-function agricultural biodiversity: pest management and other benefits. *Basic and Applied Ecology*, 4(2):107–116.
- Gurr, G. M., Wratten, S. D., and Snyder, W. E. (2012). *Biodiversity and insect pests: key issues for sustainable management*. Wiley-Blackwell, Oxford, UK.
- Hallmann, C. A., Foppen, R. P. B., van Turnhout, C. A. M., de Kroon, H., and Jongejans, E. (2014). Declines in insectivorous birds are associated with high neonicotinoid concentrations. *Nature*, 511:341–343.
- Hardy, N. B., Gullan, P. J., and Hodgson, C. J. (2008). A subfamily level classification of mealybugs (Hemiptera: Pseudococcidae) based on integrated molecular and morphological data. *Systematic Entomology*, 33:51–71.
- Harwood, J. D., Phillips, S. W., Lello, J., Sunderland, K. D., Glen, D. M., Bruford, M. W., Harper, G. L., and Symondson, W. O. C. (2009). Invertebrate biodiversity affects predator fitness and hence potential to control pests in crops. *Biological Control*, 51(3):499–506.
- Harwood, J. D., Yoo, H. J. S., Greenstone, M. H., Rowley, D. L., and O’Neil, R. J. (2008). Differential impact of adults and nymphs of a generalist predator on an exotic invasive pest demonstrated by molecular gut-content analysis. *Biological Invasions*, 11(4):895–903.
- He, X., Wang, Q., and Xu, J. (2008). European earwig as a potential biological control agent of apple leaf-curling midge. *New Zealand Plant Protection*, 349:343–349.
- Hobbs, P. R., Sayre, K., and Gupta, R. (2008). The role of conservation agriculture in sustainable agriculture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1491):543–555.
- Hogg, B. N., Wang, X. G., Levy, K., Mills, N. J., and Daane, K. M. (2013). Complementary effects of resident natural enemies on the suppression of the introduced moth *Epiphyas postvittana*. *Biological Control*, 64(2):125–131.



- Hogg, B. N., Wang, X.-G., Mills, N. J., and Daane, K. M. (2014). Resident spiders as predators of the recently introduced light brown apple moth, *Epiphyas postvittana*. *Entomologia Experimentalis et Applicata*, 151:65–74.
- Hooper, D. U., Chapin, III, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., and Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, 75(1):3–35.
- Irvin, N. A., Scarratt, S. L., Wratten, S. D., Frampton, C. M., Chapman, R. B., and Tylisanakis, J. M. (2006). The effects of floral understoreys on parasitism of leafrollers (Lepidoptera: Tortricidae) on apples in New Zealand. *Agricultural and Forest Entomology*, 8(1):25–34.
- Ives, A. R., Cardinale, B. J., and Snyder, W. E. (2005). A synthesis of subdisciplines: predator-prey interactions, and biodiversity and ecosystem functioning. *Ecology Letters*, 8(1):102–116.
- Jackson, A. C. and Underwood, A. J. (2007). Application of new techniques for the accurate analysis of choice of prey. *Journal of Experimental Marine Biology and Ecology*, 341(1):1–9.
- Jacometti, M. A., Wratten, S. D., and Walter, M. (2007). Management of understorey to reduce the primary inoculum of *Botrytis cinerea*: enhancing ecosystem services in vineyards. *Biological Control*, 40(1):57–64.
- Jonsson, M., Wratten, S. D., Landis, D. A., and Gurr, G. M. (2008). Recent advances in conservation biological control of arthropods by arthropods. *Biological Control*, 45(2):172–175.
- Kastner, T., Rivas, M. J. I., Koch, W., and Nonhebel, S. (2012). Global changes in diets and the consequences for land requirements for food. *Proceedings of the National Academy of Sciences*, 109(18):6868–6872.
- Kim, H. and Bonn, M. A. (2015). The moderating effects of overall and organic wine knowledge on consumer behavioral intention. *Scandinavian Journal of Hospitality and Tourism*, pages 1–16.
- Krebs, J. R., Wilson, J. D., Bradbury, R. B., and Siriwardena, G. M. (1995). A second silent spring? *Trends in ecology and evolution*, 10(7):611–612.
- Kuyper, T. W. and Struik, P. C. (2014). Epilogue: global food security, rhetoric, and the sustainable intensification debate. *Current Opinion in Environmental Sustainability*, 8:71–79.
- Landis, D. A. and van der Werf, W. (1997). Early-season predation impacts the establishment of aphids and spread of beet yellows virus in sugar beet. *Entomophaga*, 42(4):499–516.

- Landis, D. A., Wratten, S. D., and Gurr, G. M. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, 45(1):175–201.
- Lang, T. (2010). Crisis? What crisis? The normality of the current food crisis. *Journal of Agrarian Change*, 10(1):87–97.
- Laurin, M. C. and Bostanian, N. J. (2007). Short-term contact toxicity of seven fungicides on *Anystis baccarum*. *Phytoparasitica*, 35(4):380–385.
- Lefort, M. C., Boyer, S., Worner, S. P., and Armstrong, K. (2012). Noninvasive molecular methods to identify live scarab larvae: an example of sympatric pest and nonpest species in New Zealand. *Molecular Ecology Resources*, 12:389–395.
- Lewis, W. J., van Lenteren, J. C., Phatak, S. C., and Tumlinson, J. H. (1997). A total system approach to sustainable pest management. *Proceedings of the National Academy of Sciences*, 94:12243–12248.
- Lo, P. L. and Murrell, V. C. (2000). Time of leafroller infestation and effect on yield in grapes. *New Zealand Plant Protection*, 53:173–178.
- Lo, P. L. and Walker, J. T. S. (2011). Soil applications of two neonicotinoid insecticides to control mealybugs (Pseudococcidae) in vineyards. *New Zealand Plant Protection*, 106:101–106.
- Logan, D. P., Maher, B. J., and Connolly, P. G. (2011). Increased numbers of earwigs (*Forficula auricularia*) in kiwifruit orchards are associated with fewer broad-spectrum sprays. *New Zealand Plant Protection*, 64:49–54.
- Long, E. Y. and Finke, D. L. (2014). Contribution of predator identity to the suppression of herbivores by a diverse predator assemblage. *Environmental Entomology*, 43(3):569–576.
- Lordan, J., Alegre, S., Blanco, R., Sarasúa, M. J., and Alins, G. (2014). Aggregation behavior in the European earwig: Response to impregnated shelters. *Crop Protection*, 65:71–76.
- Loreau, M., Mouquet, N., and Gonzalez, A. (2003). Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences*, 100(22):12765–12770.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., Tilman, D., and Wardle, D. A. (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294:804 – 808.
- Losey, J. E. and Denno, R. F. (1998). Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology*, 79(6):2143–2152.

- Losey, J. E. and Vaughan, M. (2006). The economic value of ecological services provided by insects. *BioScience*, 56(4):311.
- Louda, S. M., Pemberton, R. W., Johnson, M. T., and Follett, P. A. (2003). Nontarget effects-the Achilles' heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. *Annual Review of Entomology*, 48:365–396.
- Luck, G. W., Daily, G. C., and Ehrlich, P. R. (2003). Population diversity and ecosystem services. *Trends in Ecology and Evolution*, 18(7):331–336.
- MacArthur, R. H. and Pianka, E. R. (1966). On optimal use of a patchy environment. *American Naturalist*, 100(916):603–609.
- Macfadyen, S., Gibson, R. H., Polaszek, A., Morris, R. J., Craze, P. G., Planqué, R., Symondson, W. O. C., and Memmott, J. (2009). Do differences in food web structure between organic and conventional farms affect the ecosystem service of pest control? *Ecology Letters*, 12(3):229–238.
- Manktelow, D., Stevens, P., Walker, J., Gurnsey, S., Park, N., Zabkiewicz, J., Teulon, D., and Rahman, A. (2005). Trends in pesticide use in New Zealand: 2004. Technical Report November, Ministry for the Environment, Wellington, New Zealand.
- Manly, B. F. J. (2006). On a proposed method for analysing experiments on food choice. *Journal of Experimental Marine Biology and Ecology*, 335(1):154–155.
- Mannini, F., Gerbi, V., and Credi, R. (1997). Heat-treated V. virus-infected grapevine clones: agronomical and enological modifications. In *International Symposium on the Importance of Varieties and Clones in the production of Quality Wine 473*, pages 155–164.
- Maoz, Y., Gal, S., Argov, Y., Coll, M., and Palevsky, E. (2011). Biocontrol of perseia mite, *Oligonychus perseae*, with an exotic spider mite predator and an indigenous pollen feeder. *Biological Control*, 59(2):147–157.
- Maoz, Y., Gal, S., Argov, Y., Domeratzky, S., Melamed, E., Gan-Mor, S., Coll, M., and Palevsky, E. (2014). Efficacy of indigenous predatory mites (Acari: Phytoseiidae) against the citrus rust mite *Phyllocoptruta oleivora* (Acari: Eriophyidae): augmentation and conservation biological control in Israeli citrus orchards. *Experimental and Applied Acarology*, 63(3):295–312.
- Matson, P. A., Parton, W. J., Power, A. G., and Swift, M. J. (1997). Agricultural intensification and ecosystem properties. *Science*, 277(1997):504–509.
- McMurtry, J. A., de Moraes, G. J., and Sourassou, N. F. (2013). Revision of the lifestyles of phytoseiid mites (Acari: Phytoseiidae). *Systemic and Applied Acarology*, 18(4):297–320.

- Merfield, C. N., Wratten, S. D., and Navntoft, S. (2004). Video analysis of predation by polyphagous invertebrate predators in the laboratory and field. *Biological Control*, 29(1):5–13.
- Millar, J. G., Moreira, J. A., McElfresh, J. S., Daane, K. M., and Freund, A. S. (2009). Sex pheromone of the long-tailed mealybug: a new class of monoterpene structure. *Organic Letters*, 11:2683–2685.
- Mo, J., Glover, M., Munro, S., and Beattie, G. A. C. (2006). Development of *Epiphyas postvittana* (Lepidoptera : Tortricidae) on leaves and fruit of orange trees. *Journal of Economic Entomology*, 99:1321–1326.
- Moerkens, R., Gobin, B., Peusens, G., Helsen, H., Hilton, R., Dib, H., Suckling, D. M., and Leirs, H. (2011). Optimizing biocontrol using phenological day degree models: the European earwig in pipfruit orchards. *Agricultural and Forest Entomology*, 13(3):301–312.
- Moerkens, R., Leirs, H., Peusens, G., and Gobin, B. (2009). Are populations of European earwigs, *Forficula auricularia*, density dependent? *Entomologia Experimentalis et Applicata*, 130(2):198–206.
- Mollá-Bauzá, M. B., Martínez-Carrasco, L., Martínez-Poveda, A., and Rico Pérez, M. (2005). Determination of the surplus that consumers are willing to pay for an organic wine. *Spanish Journal of Agricultural Research*, 3(1):43–51.
- Mondelaers, K., Aertsens, J., and van Huylenbroeck, G. (2009). A meta-analysis of the differences in environmental impacts between organic and conventional farming. *British Food Journal*, 111:1098–1119.
- Mueller, T. E., Blommers, L. H. M., and Mols, P. J. M. (1988). Earwig (*Forficula auricularia*) predation on the woolly apple aphid, *Eriosoma lanigerum*. *Entomologia Experimentalis et Applicata*, 47:145–152.
- Mullin, C. A., Frazier, M., Frazier, J. L., Ashcraft, S., Simonds, R., van Engelsdorp, D., and Pettis, J. S. (2010). High levels of miticides and agrochemicals in North American apiaries: implications for honey bee health. *PLoS ONE*, 5(3):1–19.
- Murdoch, W. W. . (1969). Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Modelling*, 39(4):335–354.
- Naeem, S. (1998). Species redundancy and ecosystem reliability. *Conservation Biology*, 12(1):39–45.
- Naeem, S., Ingram, J. C., Varga, A., Agardy, T., Barten, P., Bennett, G., Bloomgarden, E., Bremer, L. L., Burkill, P., Cattau, M., Ching, C., Colby, M., Cook,

- D. C., Costanza, R., Declerck, F., Freund, C., Gartner, T., Gunderson, J., Jarrett, D., Kinzig, A. P., Kiss, A., Koontz, A., Kumar, P., Lasky, J. R., Masozera, M., Meyers, D., Milano, F., Nichols, E., Olander, L., Olmsted, P., Perge, E., Perrings, C., Polasky, S., Potent, J., Prager, C., Quétier, F., Redford, K., Satterson, K., Thoumi, G., Vargas, M. T., Vickerman, S., Weisser, W., Wilkie, D., and Wunder, S. (2015). Get the science right when paying for nature's services. *Science*, 347(6227):1206–1207.
- Naeem, S., Thompson, L. J., Lawler, S. P., Lawton, J. H., and Woodfin, R. M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature*, 368:734–737.
- Nasrabadi, T., Bidhendi, G. N., Karbassi, A., Grathwohl, P., and Mehrdadi, N. (2011). Impact of major organophosphate pesticides used in agriculture to surface water and sediment quality (Southern Caspian Sea basin, Haraz River). *Environmental Earth Sciences*, 63:873–883.
- New Zealand Winegrowers (2014). New Zealand Winegrowers Annual Report. Technical report, New Zealand Winegrowers, Auckland, New Zealand.
- Nicholls, C. I., Altieri, M. A., and Ponti, L. (2008). Enhancing plant diversity for improved insect pest management in Northern California organic vineyards. In Adsule, P. G., Sawant, I. S., and Shikhamany, S. D., editors, *International Symposium on Grape Production and Processing 785*, volume 1, pages 263–278, Baramati (Pune), Maharashtra, India. ISHS Acta Horticulturae.
- Nilsson, P. A. (2001). Predator behaviour and prey density: evaluating intraspecific interactions on predator functional responses. *Journal of Animal Ecology*, 70(1):14–19.
- Northfield, T. D., Crowder, D. W., Takizawa, T., and Snyder, W. E. (2014). Pairwise interactions between functional groups improve biological control. *Biological Control*, 78:49–54.
- OIV (2014). The wine market: evolution and trends. Technical Report May, 2014, Organisation Internationale de la Vigne et du Vin, Paris, France.
- Östman, O., Ekbom, B., and Bengtsson, J. (2001). Landscape heterogeneity and farming practice influence biological control. *Basic and Applied Ecology*, 371:365–371.
- Paull, C. A., Schellhorn, N. A., HilleRisLambers, R., and Austin, A. D. (2012). Escape from parasitoids leave larvae vulnerable to predators and has unexpected outcomes for pest suppression. *Basic and Applied Ecology*, 13(6):542–550.
- Persons, M. H. (1999). Hunger effects on foraging responses to perceptual cues in immature and adult wolf spiders (Lycosidae). *Animal Behaviour*, 57:81–88.

- Petchey, O. L. and Gaston, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5(3):402–411.
- Petersen, C. L. and Charles, J. G. (1997). Transmission of grapevine leafroll-associated closteroviruses by *Pseudococcus longispinus* and *P. calceolariae*. *Plant Pathology*, 46(4):509–515.
- Petersen, C. L. and Jordan, D. (1992). ELISA works well for the identification of leafroll. In *Proceedings of the New Zealand Grape and Wine Symposium: profit in the market, in the winery, in the vineyard*, pages 54–55, Christchurch, New Zealand. New Zealand Society for Viticulture and Oenology.
- Pfannenstiel, R. S. and Yeargan, K. V. (2002). Identification and diel activity patterns of predators attacking *Helicoverpa zea* (Lepidoptera: Noctuidae) eggs in soybean and sweet corn. *Environmental Entomology*, 31(2):232–241.
- Pimentel, D., Acquay, H., Biltonen, M., Rice, P., Silva, M., Nelson, J., Lipner, V., Giordano, S., Horowitz, A., and D’Amore, M. (1992). Environmental and economic costs of pesticide use. *BioScience*, 42(10):750–760.
- Polis, G. A. and Holt, R. D. (1992). Intraguild predation: The dynamics of complex trophic interactions. *Trends in Ecology and Evolution*, 7(5):151–154.
- Polis, G. A., Myers, C. A., and Holt, R. D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics*, 20:297–330.
- Porter, J. R., Costanza, R., Sandhu, H. S., Sigsgaard, L., and Wratten, S. D. (2009). The value of producing food, energy, and ecosystem services within an agro-ecosystem. *AMBIO: A Journal of the Human Environment*, 38(4):186–193.
- Pretty, J. (2013). The consumption of a finite planet: well-being, convergence, divergence and the nascent green economy. *Environmental and Resource Economics*, 55:475–499.
- Pretty, J. and Bharucha, Z. P. (2014). Sustainable intensification in agricultural systems. *Annals of Botany*, 114(1911):1571–1596.
- R Development Core Team (2011). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rankin, S. M. and Palmer, J. O. (2009). Dermaptera: (Earwigs). In Resh, V. H. and Cardé, R. T., editors, *Encyclopedia of Insects*, chapter 70: Dermap, pages 259 – 261. Academic Press, San Diego, second edition.
- Rapport, D. J. and Turner, J. E. (1970). Determination of Predator Food Preferences. *Journal of Theoretical Biology*, 26:365–372.

- Ridsdill-Smith, T. J. (1997). Biology and control of *Halotydeus destructor* (Tucker) (Acarina: Penthaleidae): a review. *Experimental and Applied Acarology*, 21:195–224.
- Riechert, S. E. (1999). The hows and whys of successful pest suppression by spiders: insights from case studies. *Journal of Arachnology*, 27(1):387–396.
- Riechert, S. E. and Bishop, L. (1990). Prey control by an assemblage of generalist predators: spiders in garden test systems. *Ecology*, 71(4):1441–1450.
- Riechert, S. E. and Lockley, T. (1984). Spiders as biological control agents. *Annual Review of Entomology*, 29(1):299–320.
- Riechert, S. E. and Maupin, J. L. (1998). Spider effects on prey: tests for superfluous killing in five web-builders. In Selden, P. A., editor, *Proceedings of the 17th European Colloquium of Arachnology*, pages 203–210, Edinburgh, UK.
- Robinson, B., Greven, M., Green, S., Sivakumaran, S., Davidson, P., and Clothier, B. (2006). Leaching of copper, chromium and arsenic from treated vineyard posts in Marlborough, New Zealand. *The Science of the Total Environment*, 364(1-3):113–23.
- Rogers, D. J., Walker, J. T. S., Moen, I. C., Weibel, F., Lo, P. L., and Cole, L. M. (2003). Understorey influence on leafroller populations in Hawke’s Bay organic apple orchards. In Zydenbos, S. M., editor, *56th Conference Proceedings (2003) of The New Zealand Plant Protection Society Incorporated*, pages 168–173, Christchurch, New Zealand.
- Rosenheim, J. A. (2001). Source-sink dynamics for a generalist insect predator in habitats with strong higher-order predation. *Ecological Monographs*, 71(1):93–116.
- Rosenheim, J. A., Kaya, H. K., Ehler, L. E., Marois, J. J., and Jaffee, B. A. (1995). Intraguild predation among biological-control agents: theory and evidence. *Biological Control*, 5:303–335.
- Rosenheim, J. A., Wilhoit, L. R., and Armer, C. A. (1993). Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia*, 96(3):439–449.
- Rosset, P. M. and Altieri, M. A. (1997). Agroecology versus input substitution: a fundamental contradiction of sustainable agriculture. *Society and Natural Resources: An International Journal*, 10(3):283 – 295.
- Sabelis, M. W. (1992). Predatory arthropods. In Crawley, M. J., editor, *Natural Enemies: The Population Biology of Predators, Parasites and Diseases*, chapter 10, pages 225–264. Blackwell Science, Oxford, UK.

- Sandhu, H. S., Wratten, S. D., Costanza, R., Pretty, J., Porter, J. R., and Reganold, J. (2015). Significance and value of non-traded ecosystem services on farmland. *PeerJ*, 3:1–22.
- Sandhu, H. S., Wratten, S. D., and Cullen, R. (2008). The future of farming: the value of ecosystem services in conventional and organic arable land. An experimental approach. *Ecological Economics*, 4(2):835–848.
- Scarratt, S. L., Wratten, S. D., and Shishehbor, P. (2008). Measuring parasitoid movement from floral resources in a vineyard. *Biological Control*, 46(2):107–113.
- Schausberger, P. and Croft, B. A. (2000). Nutritional benefits of intraguild predation and cannibalism among generalist and specialist phytoseiid mites. *Ecological Entomology*, 25:473–480.
- Schausberger, P. and Walzer, A. (2001). Combined versus single species release of predaceous mites: predator-predator interactions and pest suppression. *Biological Control*, 20(3):269–278.
- Schmaedick, M. A. and Shelton, A. M. (2000). Arthropod predators in cabbage (Cruciferae) and their potential as naturally occurring biological control agents for *Pieris rapae* (Lepidoptera: Pieridae). *The Canadian Entomologist*, 132(5):655–675.
- Schmitz, O. J. (2007). Predator diversity and trophic interactions. *Ecology*, 88(10):2415–2426.
- Schmitz, O. J. (2009). Effects of predator functional diversity on grassland ecosystem function. *Ecology*, 90(9):2339–2345.
- Schmitz, O. J. and Sokol-Hessner, L. (2002). Linearity in the aggregate effects of multiple predators in a food web. *Ecology Letters*, 5(2):168–172.
- Schneider, F. D. and Brose, U. (2013). Beyond diversity: how nested predator effects control ecosystem functions. *The Journal of animal ecology*, 82(1):64–71.
- Settle, W. H., Ariawan, H., Astuti, E. T., Cahyana, W., Hakim, A. L., Hindayana, D., and Lestari, A. S. (1996). Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology*, 77(7):1975–1988.
- Seufert, V., Ramankutty, N., and Foley, J. A. (2012). Comparing the yields of organic and conventional agriculture. *Nature*, 485(7397):229–232.
- Sharley, D. J., Hoffmann, A. A., and Thomson, L. J. (2008). The effects of soil tillage on beneficial invertebrates within the vineyard. *Agricultural and Forest Entomology*, 10:233–243.
- Sih, A., Englund, G., and Wooster, D. (1998). Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution*, 13(9):350–355.



- Singer, M. C. (2000). Reducing ambiguity in describing plant-insect interactions: "preference", "acceptability" and "electivity". *Ecology Letters*, 3:159–162.
- Snyder, W. E. and Ives, A. R. (2001). Generalist predators disrupt biological control by a specialist parasitoid. *Ecology*, 82(3):705–716.
- Snyder, W. E. and Ives, A. R. (2003). Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. *Ecology*, 84(1):91–107.
- Snyder, W. E. and Wise, D. H. (1999). Predator interference and the establishment of generalist predator populations for biocontrol. *Biological Control*, 29:283–292.
- Sokol-Hessner, L. and Schmitz, O. J. (2002). Aggregate effects of multiple predator species on a shared prey. *Ecology*, 83(9):2367–2372.
- Solomon, M. G., Cross, J. V., Fitzgerald, J. D., Campbell, C. a. M., Jolly, R. L., Olszak, R. W., Niemczyk, E., and Vogt, H. (2000). Biocontrol of pests of apples and pears in northern and central Europe - 3. Predators. *Biocontrol Science and Technology*, 10(2):91–128.
- Soluk, D. A. (1993). Multiple predator effects: predicting combined functional response of stream fish and invertebrate predators. *Ecology*, 74(1):219–225.
- Soluk, D. A. and Collins, N. C. (1988). Synergistic and interference between fish and stoneflies: facilitation interactions among stream predators. *Oikos*, 52:94–100.
- Spencer, W. F., Singh, G., Taylor, C. D., LeMert, R. A., Cliath, M. M., and Farmer, W. J. (1996). DDT persistence and volatility as affected by management practices after 23 years. *Journal of Environmental Quality*, 25:815–821.
- Straub, C. S., Finke, D. L., and Snyder, W. E. (2008). Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biological Control*, 45(2):225–237.
- Suckling, D. M. and Brockerhoff, E. G. (2010). Invasion biology, ecology, and management of the light brown apple moth (Tortricidae). *Annual Review of Entomology*, 55:285–306.
- Suckling, D. M., Burnip, G. M., Hackett, J., and Daly, J. C. (2006). Frass sampling and baiting indicate European earwig (*Forficula auricularia*) foraging in orchards. *Journal of Applied Entomology*, 130(5):263–267.
- Suckling, D. M., Burnip, G. M., Walker, J. T. S., Shaw, P. W., McLaren, G. F., Howard, C. R., Lo, P. L., White, V., and Fraser, J. (1998). Abundance of leafrollers and their parasitoids on selected host plants in New Zealand. *New Zealand Journal of Crop and Horticultural Science*, 26:193–203.

- Suckling, D. M. and Shaw, P. W. (1995). Large-scale trials of mating disruption of lightbrown apple moth in Nelson, New Zealand. *New Zealand Journal of Crop and Horticultural Science*, 23:127–137.
- Suckling, D. M., Shaw, P. W., Khoo, J. G. I., and Cruickshank, V. (1990). Resistance management of lightbrown apple moth, *Epiphyas postvittana* (Lepidoptera: Tortricidae) by mating disruption. *New Zealand Journal of Crop and Horticultural Science*, 18:89–98.
- Sunderland, K. D. (1999). Mechanisms underlying the effects of spiders on pest populations. *Journal of Arachnology*, 27(1):308–316.
- Sunderland, K. D. and Samu, F. (2000). Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: a review. *Entomologia Experimentalis et Applicata*, 95(1):1–13.
- Symondson, W. O. C. and Harwood, J. D. (2014). Special issue on molecular detection of trophic interactions: unpicking the tangled bank. *Molecular Ecology*, 23:3601–3604.
- Symondson, W. O. C., Sunderland, K. D., and Greenstone, M. H. (2002). Can generalist predators be effective biocontrol agents? *Annual Review of Entomology*, 47(1):561–594.
- Takada, M. B., Kobayashi, T., Yoshioka, A., Takagi, S., and Washitani, I. (2013). Facilitation of ground-dwelling wolf spider predation on mirid bugs by horizontal webs built by Tetragnatha spiders in organic paddy fields. *The Journal of Arachnology*, 41(1):31–35.
- Taplin, R. H. (2007). Experimental design and analysis to investigate predator preferences for prey. *Journal of Experimental Marine Biology and Ecology*, 344(1):116–122.
- Thies, C., Haenke, S., Scherber, C., Bengtsson, J., Bommarco, R., Clement, L. W., Ceryngier, P., Dennis, C., Emmerson, M., Gagic, V., Hawro, V., Liira, J., Weisser, W. W., Winqvist, C., and Tscharrntke, T. (2011). The relationship between agricultural intensification and biological control: experimental tests across Europe. *Ecological Applications*, 21(6):2187–2196.
- Thomas, W. P. (1989). *Epiphyas postvittana* (Walker), lightbrown apple moth (Lepidoptera: Tortricidae). In Cameron, P. J., Hill, R. L., Bain, J., and Thomas, W. P., editors, *A Review of Biological Control of Invertebrate Pests and Weeds in New Zealand 1874 to 1987*. CAB International, Wallingford, UK.
- Tilman, D. (2001). Functional diversity. In Levin, S. A., editor, *Encyclopedia of Biodiversity*, pages 109–120. Academic Press, San Diego, CA, 3 edition.

- Tilman, D., Balzer, C., Hill, J., and Befort, B. L. (2011). Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences*, 108(50):20260–20264.
- Tilman, D., Cassman, K. G., Matson, P. A., Naylor, R., and Polasky, S. (2002). Agricultural sustainability and intensive production practices. *Nature*, 418(6898):671–677.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., and Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, 277:1300–1302.
- Tompkins, J. M. L. and Mason, P. G. (2008). Endemic New Zealand plants for pest management in vineyards. In Mason, P. G., Gillespie, D. R., and Vincent, C., editors, *Proceedings of the Third International Symposium on Biological Control of Arthropods*, pages 234 – 245, Chrsitchurch, New Zealand.
- Tooman, L. K., Rose, C. J., Carraher, C., Suckling, D. M., Paquette, S. R., Bastien, R., Ledezma, L. A., Gilligan, T. M., Epstein, M., Barr, N. B., and Newcomb, R. D. (2011). Patterns of mitochondrial haplotype diversity in the invasive pest *Epiphyas postvittana* (Lepidoptera: Tortricidae). *Journal of Economic Entomology*, 104(3):920–932.
- Topping, C. J. and Sunderland, K. D. (1992). Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *Journal of Applied Ecology*, 29(2):485–491.
- Tscharntke, T., Clough, Y., Wanger, T. C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., and Whitbread, A. (2012). Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation*, 151(1):53–59.
- Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., and Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters*, 8(8):857–874.
- Turusov, V., Rakitsky, V., and Tomatis, L. (2002). Dichlorodiphenyl-trichloroethane (DDT): ubiquity, persistence, and risks. *Environmental Health Perspectives*, 110(2):125–128.
- Tylianakis, J. M. and Romo, C. M. (2010). Natural enemy diversity and biological control: making sense of the context-dependency. *Basic and Applied Ecology*, 11(8):657–668.
- Uetz, G. W., Halaj, J., and Cady, A. B. (1999). Guild structure of spiders in major crops. *Journal of Arachnology*, 27(1):270–280.

- Underwood, A. J., Chapman, M. G., and Crowe, T. P. (2004). Identifying and understanding ecological preferences for habitat or prey. *Journal of Experimental Marine Biology and Ecology*, 300:161–187.
- Underwood, A. J. and Clarke, K. R. (2005). Solving some statistical problems in analyses of experiments on choices of food and on associations with habitat. *Journal of Experimental Marine Biology and Ecology*, 318(2):227–237.
- Underwood, A. J. and Clarke, K. R. (2006). Response on a proposed method for analysing experiments on food choice. *Journal of Experimental Marine Biology and Ecology*, 335(1):151–153.
- Unelius, C. R., El-Sayed, A. M., Twidle, A., Bunn, B., Zaviezo, T., Flores, M. F., Bell, V. A., and Bergmann, J. (2011). The absolute configuration of the sex pheromone of the citrophilous mealybug, *Pseudococcus calceolariae*. *Journal of Chemical Ecology*, 37:166–172.
- van der Sluijs, J. P., Simon-Delso, N., Goulson, D., Maxim, L., Bonmatin, J. M., and Belzunces, L. P. (2013). Neonicotinoids, bee disorders and the sustainability of pollinator services. *Current Opinion in Environmental Sustainability*, 5(3-4):293–305.
- Vance-Chalcraft, H. D., Rosenheim, J. A., Vonesh, J. R., Osenberg, C. W., and Sih, A. (2007). The influence of intraguild predation on prey suppression and prey release: a meta-analysis. *Ecology*, 88(11):2689–2696.
- Vance-Chalcraft, H. D. and Soluk, D. A. (2005a). Estimating the prevalence and strength of non-independent predator effects. *Oecologia*, 146(3):452–60.
- Vance-Chalcraft, H. D. and Soluk, D. A. (2005b). Multiple predator effects result in risk reduction for prey across multiple prey densities. *Oecologia*, 144(3):472–80.
- Varela, L. G., Walker, J. T. S., Lo, P. L., and Rogers, D. J. (2008). New Zealand lessons may aid efforts to control light brown apple moth in California. *California Agriculture*, 64(1):6–12.
- Vink, C. J., Teulon, D. A. J., and McLachlan, A. R. G. (2004). Spiders (Araneae) and harvestmen (Opiliones) in arable crops and grasses in Canterbury, New Zealand. *New Zealand Journal*, 31:149–159.
- VSN International (2011). GenStat for Windows 15th Edition.
- Wakgari, W. M. and Giliomee, J. H. (2003). Natural enemies of three mealybug species (Hemiptera: Pseudococcidae) found on citrus and effects of some insecticides on the mealybug parasitoid *Coccidoxenoides peregrinus* (Hymenoptera: Encyrtidae) in South Africa. *Bulletin of Entomological Research*, 93:243–254.

- Wandel, M. and Bugge, A. (1997). Environmental concern in consumer evaluation of food quality. *Food Quality and Preference*, 8(1):19–26.
- Warner, K. D. (2007). The quality of sustainability: Agroecological partnerships and the geographic branding of California winegrapes. *Journal of Rural Studies*, 23:142–155.
- Waterworth, R. A., Redak, R. A., and Millar, J. G. (2011). Pheromone-baited traps for assessment of seasonal activity and population densities of mealybug species (Hemiptera: Pseudococcidae) in nurseries producing ornamental plants. *Journal of Economic Entomology*, 104(2):555–565.
- Wilby, A., Villareal, S. C., Lan, L. P., Heong, K. L., and Thomas, M. B. (2005). Functional benefits of predator species diversity depend on prey identity. *Ecological Entomology*, 30:497–501.
- Winqvist, C., Bengtsson, J., Aavik, T., Berendse, F., Clement, L. W., Eggers, S., Fischer, C., Flohre, A., Geiger, F., Liira, J., Pärt, T., Thies, C., Tschardtke, T., Weisser, W. W., and Bommarco, R. (2011). Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. *Journal of Applied Ecology*, 48(3):570–579.
- Wise, D. H., Moldenhauer, D. M., and Halaj, J. (2006). Using stable isotopes to reveal shifts in prey consumption by generalist predators. *Ecological Applications*, 16(3):865–876.
- Wright, J. P., Naeem, S., Hector, A., Lehman, C., Reich, P. B., Schmid, B., and Tilman, D. (2006). Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecology letters*, 9(2):111–120.
- Yardim, E. N. and Edwards, C. A. (1998). The influence of chemical management of pests, diseases and weeds on pest and predatory arthropods associated with tomatoes. *Agriculture, Ecosystems and Environment*, 70(1):31–48.
- Zaviezo, T., Cadena, E., Flores, M. F., and Bergmann, J. (2010). Influence of different plants substrates on development and reproduction for laboratory rearing of *Pseudococcus calceolariae* (Maskell) (Hemiptera: Pseudococcidae). *Ciencia e Investigación Agraria*, 37(3):31–37.
- Zehnder, G., Gurr, G. M., Kühne, S., Wade, M. R., Wratten, S. D., and Wyss, E. (2007). Arthropod pest management in organic crops. *Annual review of entomology*, 52:57–80.

*carum*, with little difference between *F. auricularia* and *P. opilio* across management types (Figure 2.3). However, the interaction between management type and predator species was not significant ( $p = 0.113$ ). No other interactions between management type and other factors were significant, either.

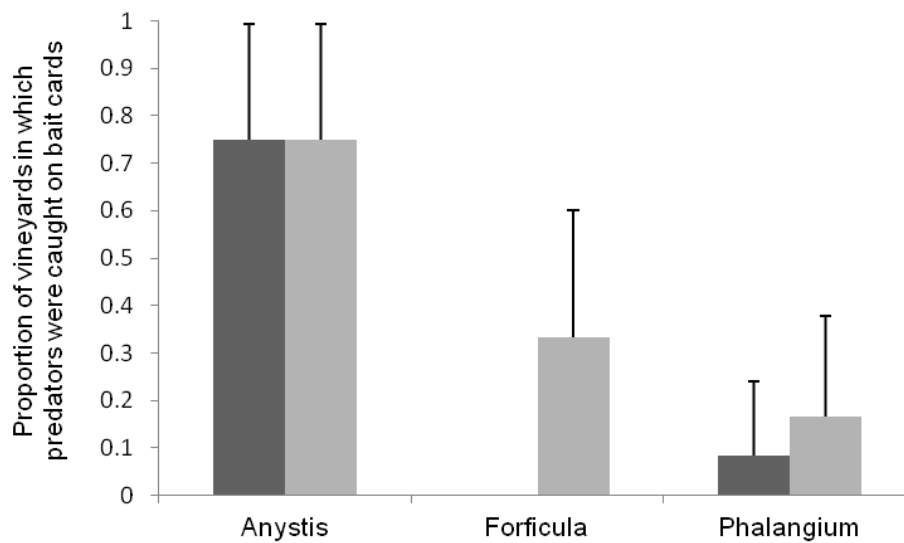


Figure 2.2: Proportion of vineyards each predator species (95% CI) were observed and collected from bait cards of *E. postvittana* eggs (dark) ( $n = 12$ ) and *E. postvittana* larvae (light) ( $n = 12$ ).

The changes between predator species found on bait cards in successive seasons were significant ( $p < 0.001$ ), possibly due to the increase of *A. baccharum* observations and absence of *P. opilio* in the 2012 season (Figure 2.4). *F. auricularia* was present in similar proportions of sites over both years (Figure 2.4).

No clear relationships occurred between *E. postvittana* consumption rates and seasons (Figure 2.5) or vineyard management (Figure 2.6). The potentially higher predation rate of *E. postvittana* larvae in conventionally managed vineyards ( $\bar{x} = 0.63$ ) than in organic vineyards ( $\bar{x} = 0.52$ ) was not significant ( $F = 3.81$ ,  $p =$

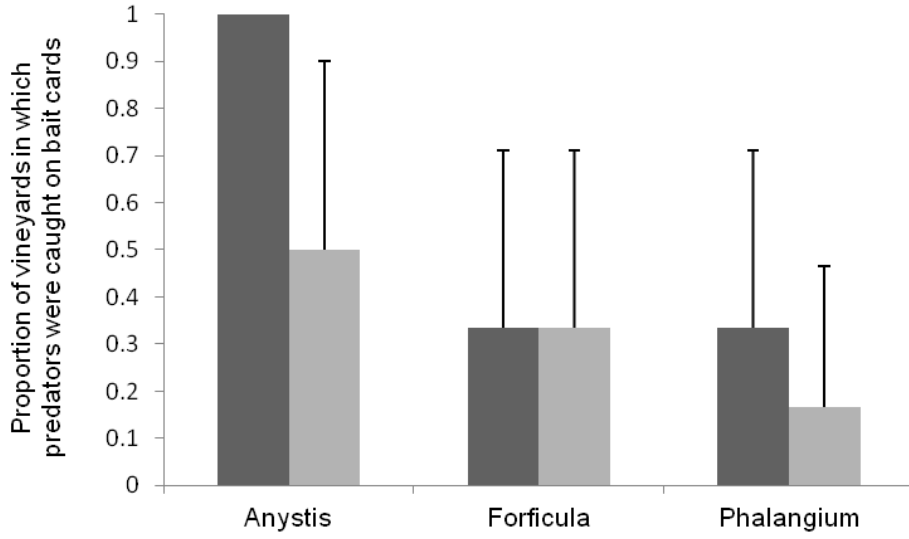


Figure 2.3: Proportion of vineyards on which each predator species (95% CI) were observed and collected from bait cards of *E. postvittana* eggs and *E. postvittana* larvae in vineyards in organic conversion (dark) and conventionally managed vineyards (light).

0.099). The interaction between the vineyard management type and season was also not significant ( $F = 4.58$ ,  $p = 0.076$ ), despite the possible drop in larvae predation in the 2012 season (Figure 2.5). Area of *E. postvittana* egg masses removed was potentially higher in organic vineyards ( $\bar{x} = 6.13 \text{ mm}^2$ ) than in conventional vineyards ( $\bar{x} = 0.85 \text{ mm}^2$ ) (Figure 2.6) though this difference was also not quite significant ( $F = 5.44$ ,  $p = 0.058$ ).

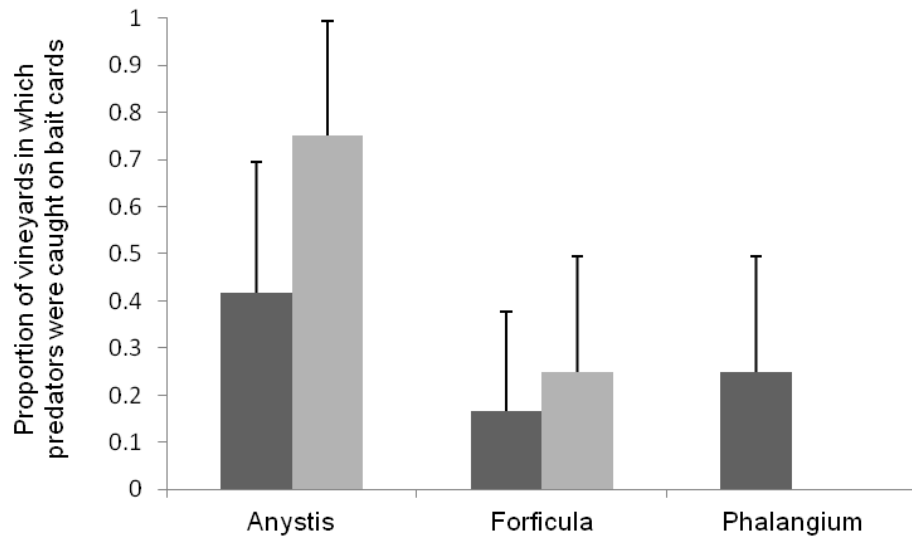


Figure 2.4: Proportion of vineyards each predator species (95% CI) observed and collected from bait cards of *E. postvittana* eggs and *E. postvittana* larvae in vineyards in 2011 (dark) (n = 12) and 2012 (light) (n = 12).

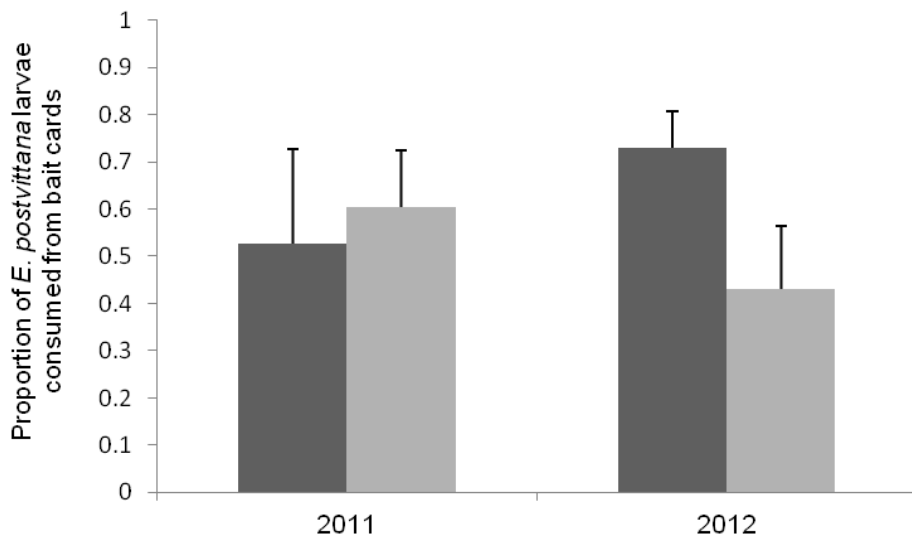


Figure 2.5: Proportion of *E. postvittana* larvae consumed (95% CI) from bait cards in conventionally managed vineyards (dark) (n = 6) and vineyards in organic conversion (light) (n = 6) in the 2011 and 2012 harvest seasons.



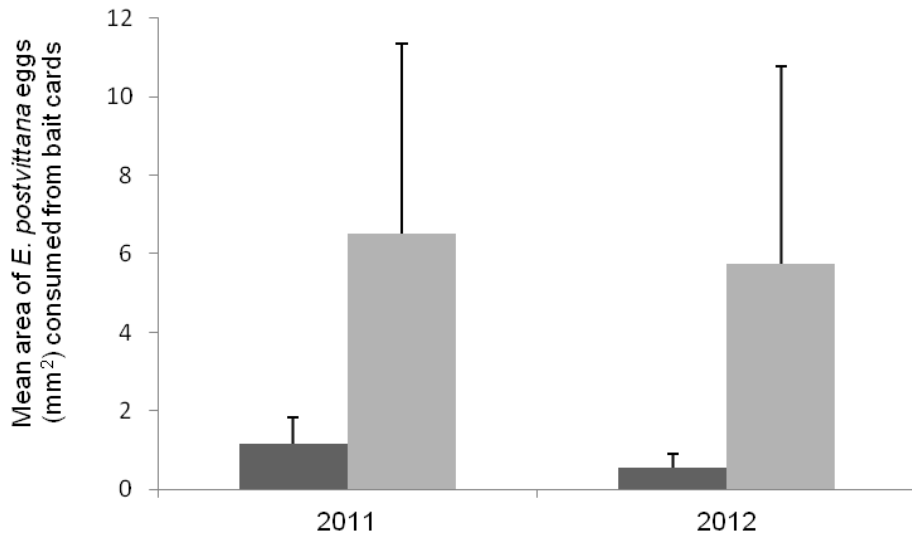


Figure 2.6: Mean consumption rate of *E. postvittana* egg mass area (mm<sup>2</sup>) from bait cards (95% CI) in conventionally managed vineyards (dark) (n = 6) and vineyards in organic conversion (light) (n = 6) in the 2011 and 2012 harvest seasons.

## 2.4 Discussion

CBC relies on identifying and engaging potential biological control agents that are already present in an ecosystem. To investigate the suitability of generalist invertebrate predators as CBC agents of *E. postvittana*, it was necessary to establish what predator species are present and which of those predated on this pest species. Consumption rates of the immature forms of the *E. postvittana*, and how the management of the vineyard influenced the predator diversity composition and their impact on *E. postvittana* were the aspects of vineyard ecology examined. Organic vineyard management and season appeared to influence predator diversity and the activity of predators consuming *E. postvittana*. The consumption of the baits used in the vineyard can be attributed largely to *A. baccharum*, *F. auricularia* and *P. opilio* from the observations made in this study. Not all predation events would have been observed, so infrequent predators of *E. postvittana* or predator

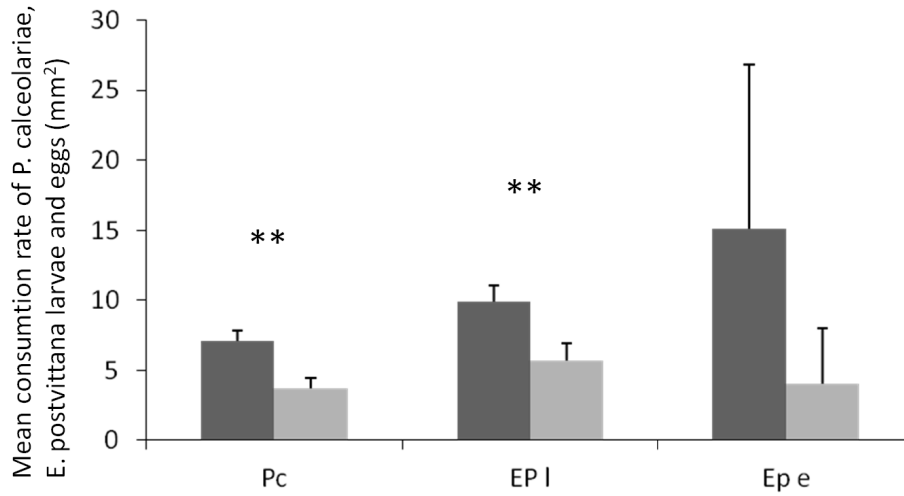


Figure 4.1: Observed mean consumption rate (95% CI) of *Ps. calceolariae* nymphs (Pc), *E. postvittana* larvae (Ep l) and egg masses (Ep e) (mm<sup>2</sup>) by *F. auricularia* (dark) and *P. opilio* (light) over 24 hours in field arenas (\*  $\geq 0.05$ , \*\*  $\geq 0.01$ ).

## 4.4 Discussion

Prey selection and preference has particular relevance in evaluating generalist predators as potential biological control agents. The experiments in this chapter were used to examine if predator species that had been identified in the laboratory as predators of the vineyard pests, *E. postvittana* and *Ps. calceolariae*, displayed frequency-related prey selection or if a stronger underlying prey preference influence of the consumption rates of the pest in a field-like setting. *F. auricularia* and *P. opilio* were the only species that were observed consuming *E. postvittana* from bait cards in vineyards and also consumed *Ps. calceolariae* in the laboratory experiments. Consumption in these trials bore more relevance to a open natural system because habitat complexity was incorporated into the design and *Ps. calceolariae* consumption was compared with a known prey species *E. postvittana*.

### 5.3 Results

Larvae predation in both pairwise predator treatments with *A. baccharum* and either *P. opilio* ( $\bar{x} = 0.40$ ) or *F. auricularia* ( $\bar{x} = 0.56$ ) had significantly higher consumption rates than the hypothesised proportions ( $\bar{x} = 0.35$   $t = 3.03$ ,  $d.f. = 4$ ,  $p = 0.039$ ; and  $\bar{x} = 0.47$ ,  $t = 4.96$ ,  $d.f. = 4$ ,  $p = 0.008$ , respectively). There was no significant difference in the proportion of larvae predated on in the treatment of *P. opilio* and *F. auricularia* from the estimated ( $t = -0.42$ ,  $d.f. = 4$ ,  $p = 0.690$ ), or with all three predator species ( $t = -1.58$ ,  $d.f. = 4$ ,  $p = 0.190$ ). Predation of larvae by single predator species varied significantly ( $p = 0.000$ ,  $F = 72.11$ ), *F. auricularia* was the highest predator of larvae and *A. baccharum* the lowest (Figure 5.5, A).

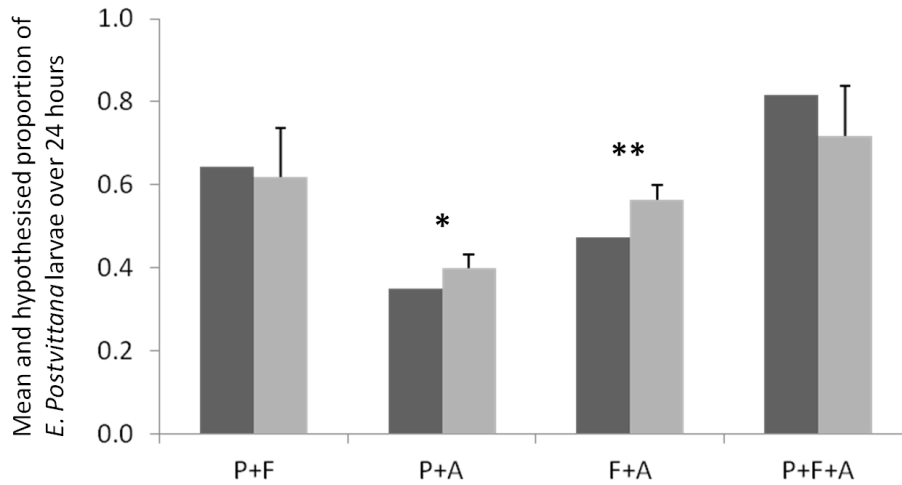


Figure 5.2: Hypothesised (dark) and observed (light) (95% CI) mean proportion of *E. postvittana* larvae consumed over 24 hours in vineyard field cages by; *P. opilio* and *F. auricularia* (P+F), *P. opilio* and *A. baccharum* (P+A), *F. auricularia* and *A. baccharum* (F+A), and *P. opilio*, *F. auricularia* and *A. baccharum* (P+F+A) (\*  $\geq 0.05$ , \*\*  $\geq 0.01$ ).

The proportion of *E. postvittana* egg masses predated on by *F. auricularia* in

combination with either *P. opilio* ( $\bar{x} = 0.09$ ) or *A. baccharum* ( $\bar{x} = 0.05$ ) were both significantly lower than the hypothesised consumption rates ( $\bar{x} = 0.20$ ,  $t = -3.42$ ,  $d.f. = 6$ ,  $p = 0.014$ , and  $\bar{x} = 0.20$ ,  $t = -6.03$ ,  $d.f. = 6$ ,  $p = 0.001$  respectively) (Figure 5.3). There was no significant interaction between *P. opilio* and *A. baccharum* or three predator species treatment that affected *E. postvittana* egg predation. *F. auricularia* had the highest consumption rate ( $p = 0.001$ ,  $F = 11.27$ ), but no significant difference was observed between *P. opilio* and *A. baccharum* consumption rates (Figure 5.5, B).

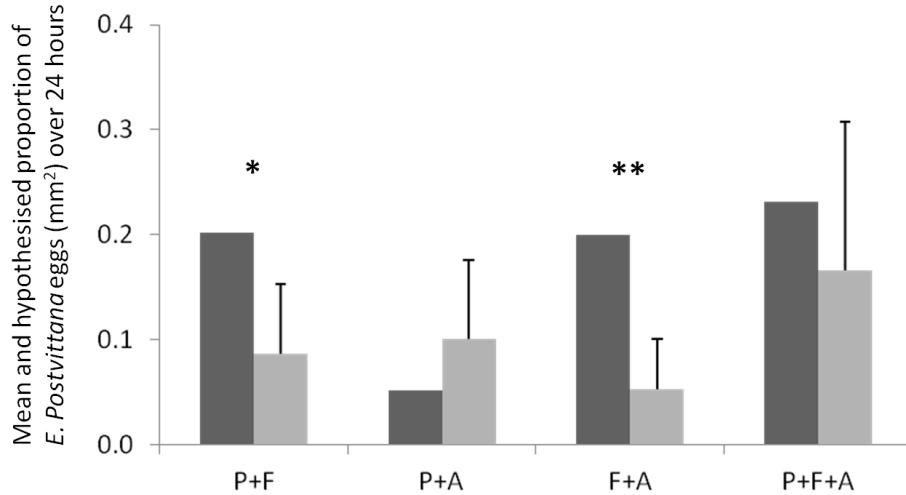


Figure 5.3: Hypothesised (dark) and observed (light) (95% CI) mean proportion of *E. postvittana* egg mass area (mm<sup>2</sup>) consumed over 24 hours in vineyard field cages by; *P. opilio* and *F. auricularia* (P+F), *P. opilio* and *A. baccharum* (P+A), *F. auricularia* and *A. baccharum* (F+A), and *P. opilio*, *F. auricularia* and *A. baccharum* (P+F+A) (\*  $\geq 0.05$ , \*\*  $\geq 0.01$ ).

The only interaction between predator species that significantly influenced *Ps. calceolariae* nymph consumption rates was the *F. auricularia* and *P. opilio* treatment ( $\bar{x} = 0.40$ ) being significantly lower than the hypothesised consumption rate ( $\bar{x} = 0.55$ ,  $t = -4.16$ ,  $d.f. = 5$ ,  $p = 0.009$ ) (Figure 5.4). In all treatments that included *A. baccharum* there was no observed affect from any predator interaction

on *Ps. calceolariae* predation. Comparisons of consumption rates of nymphs in single predator treatments ( $p = 0.000$ ,  $F = 45.82$ ), found *P. opilio* and *F. auricularia* were similar but none were predated on by *A. baccharum* (Figure 5.5, C).

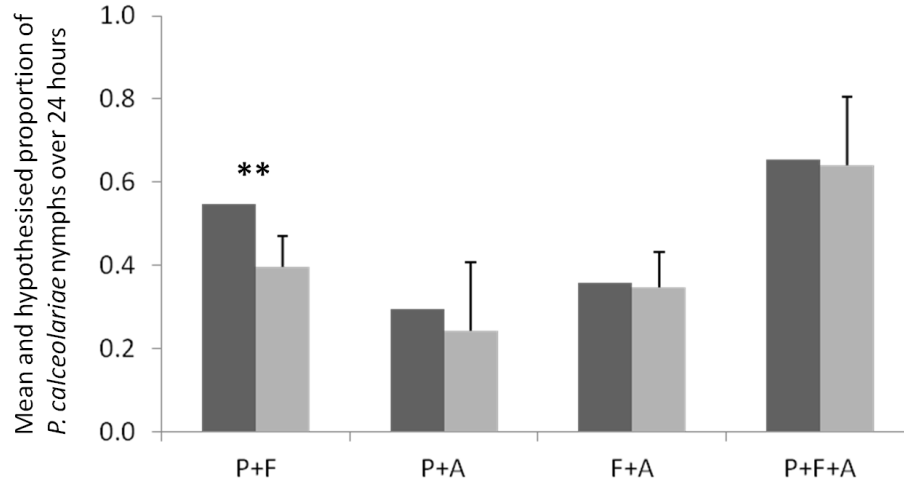


Figure 5.4: Hypothesised (dark) and observed (light) (95% CI) mean proportion of adult female *Ps. calceolariae* consumed over 24 hours in vineyard field cages by; *P. opilio* and *F. auricularia* (P+F), *P. opilio* and *A. baccharum* (P+A), *F. auricularia* and *A. baccharum* (F+A), and *P. opilio*, *F. auricularia* and *A. baccharum* (P+F+A) (\*  $\geq 0.05$ , \*\*  $\geq 0.01$ ).

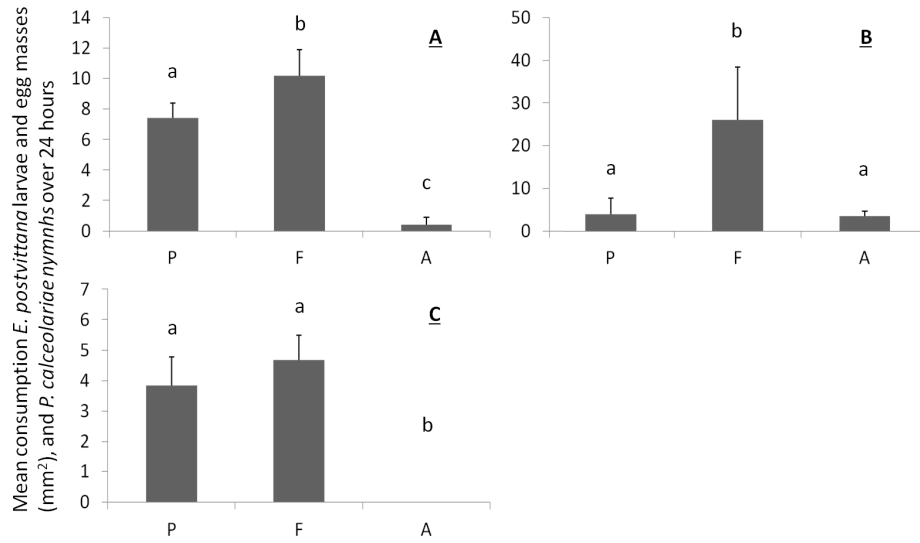


Figure 5.5: Mean consumption rates in vineyard field cages over a 24 hour period (95% CI) of *E. postvittana* larvae (A) and eggs (mm<sup>2</sup>) (B), and *Ps. calceolariae* nymphs (C) by *P. opilio* (P), *F. auricularia* (F) and *A. baccharum* (A).

## 5.4 Discussion

By using these simplified assemblages of predator and prey species, it was possible to identify the nature of the interactions between these predators of *E. postvittana* in vineyards cages. A range of synergistic, neutral and antagonistic interactions were observed amongst the various combinations of predator and prey types. Predator interactions are complex and difficult to predict, but by these basal relationships can be used to indicate how promoting one species or the other might affect the pest population in the presence of intra-guild predator species (Schneider and Brose, 2013; Chailleux et al., 2014).

Across the three prey types presented, the only consistent outcome of additive predator interactions occurred when all three predator species, *P. opilio*, *F. auricularia* and *A. baccharum* were combined. *E. postvittana* larvae were the only prey with which *P. opilio* and *F. auricularia* did not interact antagonistically, but